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Phosphorus supply alters tuber composition, flower production, and mycorrhizal responsiveness of container-grown hybrid *Zantedeschia*

C.F. Scagel[1,2] & R.P. Schreiner[1]
[1]*USDA-ARS-Horticultural Crops Research Laboratory, 3420 NW Orchard Avenue, Corvallis, OR, 97330, USA.* [2]*Corresponding author**

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Abstract

One-year old tubers of two hybrid calla lily (calla) cultivars (*Zantedeschia* 'Pot of Gold' and 'Majestic Red') were inoculated with the arbuscular mycorrhizal fungus (AMF), *Glomus intraradices*, or not, and grown at three different rates of phosphorus (P) supply to asses the effects of AMF-inoculation on plant development (time of shoot emergence and flowering), flowering (number, length and rate of flowering), and tuber biomass and composition over two growing cycles (2002, 2003). Tubers and flowers of calla responded differently to AMF inoculation. Differences in mycorrhizal responsiveness between cultivars was related to differences in P requirements for flower and tuber production, and the influence of P supply on resource allocation to different reproductive strategies. Inoculation increased shoot production and promoted early flowering, particularly in 2003. Inoculated plants also produced larger tubers than non-inoculated plants, but only increased the number of flowers per plant in 2003. High P supply also increased tuber biomass, but decreased the number of flowers per plant in 2002. Plants grown at a moderate P-rate, produced the most flowers in 2003. For 'Majestic Red', benefits from AMF were primarily in terms of tuber yield and composition, and AMF effects on marketable flower production could potentially have negative impact on production strategies for growers. Inoculation of 'Pot of Gold' primarily influenced flower production and aspects of tuber quality that caused detectable enhancement of tuber yield and flowering in the second growing cycle following inoculation (2003). The results of this study show that the responses of calla to AMF are partially a function of how nutrient supply alters resource allocation to sexual and vegetative reproduction. Whether AMF-induced changes in resource allocation to flowering and tubers significantly alters commercial productivity and quality of calla depends on the crop production goals (e.g. tubers, cut flowers or potted plants).

Introduction

The production goals of calla lily (*Zantedeschia* spp. and hybrids; also known as calla) growers depend on the products that they sell (e.g. tubers, cut flowers and potted plants). Optimizing production systems to achieve specific goals requires knowledge of how resources are partitioned during plant development. The primary goal of calla tuber growers is to produce, in the shortest time, as many tubers as possible that will provide multiple flowered, quality plants, capable of flowering during given market periods. The goal of cut flower growers of calla is to maximize flower production on a specific time schedule, and

* FAX No: + 1-541-738-4025.
E-mail: scagelc@onid.orst.edu

optimizing tuber quality for a specific number of production cycles. The goal of growers of potted calla plants is to on maximizing flower production and plant appearance within a given timeframe with less emphasis on tuber quality. When growers of one crop have such diverse goals, generalizing the influence of arbuscular mycorrhizal fungi (AMF) on crop production and quality is difficult.

Inoculation with AMF can increase productivity and quality of several commercially important floral geophytes (bulb, corm or tuber producing plants), including wild hyacinth (*Brodiaea laxa*), zephyr lilies (*Zephyranthes* spp.), Freesia (*Freesia x hybrida*), and harlequin flower (*Sparaxis tricolor*) (Scagel, 2004a, b; 2003a, b). AMF can effect bulb weight and composition, flower number and longevity, and initiation of anthesis. Inoculation has also been shown to influence allocation of carbon and nutrients between leaves and flowering structures in some species, causing changes in plant form and development. Such changes suggest that although reserves in bulbs are important for growth after planting, the effects of AMF-inoculation on plant development can independently influence growth and flowering characteristics important during commercial crop production.

Information describing the influence of AMF on vegetative reproduction of geophytes is conflicting. For example, Koch et al. (1997) reported that inoculation of garlic (*Allium sativum* L.) increased yield in fumigated soil, while Sari et al. (2002) found that it had no effect on either growth or yield (though it did improve P uptake) in low P soil. Al-Karaki (2002) observed that mycorrhizal benefits to garlic depended on soil P availability and Charron et al. (2001) made similar observations with onion (*Allium cepa* L.). Niemira et al. (1995) found, however, that AMF increased yield in potato (*Solanum tuberosum* L.) even though plants showed low root colonization levels and no evidence of enhanced P uptake. They concluded that hormones mediated the yield response of potato to AMF.

To our knowledge, there is no information on the establishment and function of mycorrhizal symbioses in non-liliaceous tuber crops used for floral crop production. However, mineral nutrition can influence such tuberous floral crops as calla, effecting both tuber yield and flower production. For example, Clemens et al. (1998) found that high nitrogen (N) reduced tuber size and subsequent flowering performance in the following growing cycle, while moderate to low N, P, and potassium (K) increased flower production and reduced time to harvest. Since AMF can increase the efficiency of uptake and use of different nutrients, especially P (Clark and Zeto, 2000), the potential effects of AMF on nutrient and carbon allocation patterns of calla could influence vegetative multiplication, flowering, and ultimately impact crop productivity and product quality. Most prior studies assessing the influence of AMF on floral geophytes (Scagel, 2004a, b; 2003a, b) have not addressed whether mycorrhizal response of the plants was a result of altered P nutrition.

The objective of this study was to determine if AMF inoculation influences plant development, reproduction (vegetative and floral), and/or tuber quality in calla lily. Plants were grown with or without mycorrhizal inoculum at different rates of P-supply in order to separate P-mediated effects from any non-P-mediated effects of the mycosymbiont. Based on previous observations on other tuberous crops, we hypothesized that increasing P supply would decrease mycorrhizal responsiveness in calla lily.

Materials and methods

Mycorrhizal inoculum

Glomus intraradices Schenck and Smith was originally obtained from Native Plants Incorporated, (Salt Lake City, Utah, USA) and maintained in pot cultures. The fungus was propagated in pot cultures on roots of bunching onion (*Allium cepa* L. 'White Lisbon') grown in 1:1 mixture of Willamette Valley alluvial silt loam and river sand (8 mg kg^{-1} available phosphorus, pH 6.3) for 5 months. Inoculum consisted of a mixture of the soil medium, extraradical hyphae and spores, and colonized root segments (< 2 mm in length). Propagule numbers (10 propagules g^{-1} of soil medium) in the inoculum used in this study were estimated using the MPN method (Woomer, 1994).

Plant material and growth conditions

One-year-old, field-grown hybrid calla (*Zantedeschia* spp.) tubers (3.8–4.4 cm), 'Pot of Gold' and

'Majestic Red', were obtained from a commercial storage facility and planted individually into 3.78-l cylindrical pots (19.4×18.1 cm, Lerio Corp., Mobile, Ala., USA) containing a steam pasteurized (60 °C for 30 min) 1:1:1:1 mixture of Willamette Valley alluvial silt loam, composted fir bark (Whitney Farms, Independence, Ore., USA), sphagnum peat (Sunshine Grower Grade White, SunGrow, Hubbard, Ore., USA), and perlite (Coarse Horticultural Grade, Supreme Perlite Company, Portland, Ore., USA). Available P (Bray) in the growing medium was 3 mg kg^{-1}, and pH was 6.2. Each tuber was planted ~3 cm deep with 20 ml of mycorrhizal inoculum (Inoculated) or 52 g of sterile (121 °C, 15 min) inoculum (Non-inoculated) placed beneath the tuber. Tubers were pretreated during storage with a mixed solution of fungicides and growth hormones containing 37.5% copper hydroxide (20 ml l^{-1}), copper oxychloride (3 g l^{-1}), 1.8% Promalin® (5.5 ml l^{-1}; Valent BioSciences Corporation, Walnut Creek, Calif., USA), and 4% Progibb (3.1 ml l^{-1}; Valent BioSciences Corporation, Walnut Creek, Calif., USA). Root fragments were removed from a subsample of tubers prior to planting and analyzed for percent mycorrhizal colonization as described below. Root fragments on tubers from grower showed <3% root colonization by AMF.

Pots were placed in a glass house and watered as needed. Supplemental light (~720 μmol PAR m^{-2} s^{-1}) was provided 15 h d^{-1} by high-pressure multi-vapor lamps. Day/night temperatures were controlled at ~24/18 °C during the first 4-weeks after planting and ~18/13 °C thereafter. Once leaf emergence began, plants were fertilized weekly with 50 ml of a liquid fertilizer containing (mg l^{-1}) 120 N, 100 K, 64 S, 100 Ca, 36 Mg, 4.6 Fe, 18 Cl, 0.55 Mn, 0.37 B, 0.024 Zn, 0.06 Cu, and 0.006 Mo, with (1) no additional P (low P), (2) 7.5 mg l^{-1} P (moderate P) or (3) 15 mg l^{-1} P (high P). P-rates were selected based on grower input of the range of P used in production. Pest control was applied as needed in the greenhouse and included Diflubenzuron for fungus gnats (*Bradysia* spp.), *Neoseiulus fallacis* predators for spider mites (*Tetranychus* spp.), and *Neoseiulus cucumeris* predators for thrips (*Frankiniella* spp.).

At the end of the first growing cycle, tubers were separated from aboveground portions of the plant and removed from the growing medium, cured 7 d at 25 °C and 80% RH, and then stored at 8 °C and 80% RH for 10 weeks. After storage, tubers were re-planted into fresh growing medium and grown for a second cycle under similar conditions as the first growing cycle, but without additional AMF inoculum. Copper fungicide treatments or growth regulators were not used in the second growing cycle.

Measurements

Shoot and flower emergence dates were recorded for each plant during two growing cycles (2002, n = 16; 2003, n = 8). The number of fully expanded flowers and marketable flowers (flowers without any browning on spathe or spadix) on each plant was recorded. The term "flower" as used in this study refers to the combination of the spadix (carrying both true male and female flowers) and a colored bract known as the spathe (Funnell, 1993). After flowering, senescent foliage (shoots and leaves) was removed from each tuber, oven-dried at 60 °C for 2 d, and weighed. Tubers were weighed before curing after the first growing cycle (2002) and tuber dry weight was calculated based on oven-dry (60 °C) weight to fresh weight ratio of tuber samples taken for chemical analysis. Dry (60 °C) weight of tubers was recorded after the second growing cycle (2003). All roots were removed from tubers in all treatments prior to curing or drying, cut into 1-cm sections, cleared, and stained, and quantified for percent root length colonized by AMF as in Biermann and Linderman (1980).

Chemical analysis of randomly selected tubers (n = 8) was conducted at the end of the first growing cycle (2002). Tubers were divided longitudinally in half; one half of each tuber was oven-dried (60 °C) while the other half was frozen in liquid N, homogenized (Polytron® PT 1300D, Brinkmann Instruments, Westbury, NY, USA), and stored at −70 °C. Oven-dried tubers were ground (60 mesh) and analyzed for N and S using automated combustion, and for P, K, Ca, Mg, Mn, B, Fe, Cu, and Zn using dry-ash oxidation and ICP-AES (Gavlak et al., 1994). Frozen tubers were analyzed for soluble protein, amino acids, glucose, fructose, sucrose, and starch. Protein concentrations were determined colorimetrically using a bicinchoninic acid assay (Smith, 1985) after extraction of ground (<50

mesh) tuber tissue in buffer (20 mM Tris, 10 mM NaCl, 10 mM KCl, 2 mM $MgCl_2 \cdot 6H_20$) with Igepal® CA-630 (octylphenoxypolyethoxyethanol). Protein data is expressed as the concentration of amino acids from protein per dry weight of tuber. Amino acid concentrations were determined colorimetrically with ninhydrin (Yemm and Cocking, 1955) after extraction of ground (<50 mesh) tuber tissue with acetic acid prior to analysis. Concentrations of soluble sugars and starch were determined colorimetrically using the specific enzyme analyses outlined in Yang et al. (2002). Briefly, two replicate samples from ground (<50 mesh) tuber tissue were extracted with 80% ethanol at 80 °C and centrifuged at 2200 rpm for 5 min. Supernatants were analyzed enzymatically for reducing sugars (glucose and fructose) and sucrose using Hexokinase (Sigma #G2020), Glucose-6-Phosphate Dehydrogenase (Sigma #G6378), Phosphoglucose Isomerase (Sigma #P5381), and Invertase (Sigma #I9374). The residual pellets left after ethanol extraction were extracted with 1 M KOH with DMSO and used to determine soluble starch concentrations after hydrolysis with Amyloglucosidase (from *Aspergillus niger* – Sigma #S9144) for 24 h at 55 °C. Sugar and starch concentrations are reported as glucose equivalents per dry mass of tuber.

Experimental design and statistical analyses

Treatments were arranged in a completely randomized design (2002, n = 16; 2003, n = 8). Data for aboveground biomass, shoot emergence, shoot number, tuber biomass, time of flowering, and number of flowers were subjected to separate Analysis of Variance (ANOVA) for each growing cycle. Mycorrhizal colonization of non-inoculated plants was <2% in both growing cycles (data not shown); therefore only colonization data from inoculated plants were statistically analyzed. Tuber biomass and composition data (2002) were subjected to ANOVA. Root colonization, number of stems, total number of flowers, and nutritional data were square-root transformed prior to analysis to correct for unequal variance and achieve best model fit. Tables and figures show back-transformed means. Means were separated using Bonferroni's Test and predetermined polynomial contrasts were used to assess whether effects were a function of P-supply and whether cultivars responded differently to treatments.

Flower production and senescence data (2002) were examined using non-linear regression to assess treatment influences on the number of marketable flowers, duration of flowering, time of peak flowering, rate of flower production and senescence. Log-normal equations ($y = y_o + a(\exp[-0.5(\ln[x-b]/c)^2])$; where y_o = baseline, a = amplitude from baseline, and $b = x$ at maximum y) were fitted to marketable flower data and parameters from the fitted equations were used to estimate the maximum number of marketable flowers (a), time of peak flowering (days after planting, DAP) (b), and duration of flowering (days) (duration = $b \exp[c(2 \ln 2)^{0.5}] - b \exp[-c(2 \ln 2)^{0.5}]$). Logistic equations ($y = y_o + [a/(1 + [x-b]^c)]$); where y_o = baseline, a = transition height from baseline, and b = transition center) were fitted to expanded and senescent flower data and parameters from fitted equations were used to estimate rate of flower production and senescence ($[a-1]/[b(3^{-1/c} - 3^{1/c})]$; flowers d^{-1}). Differences in parameters and derived variables between treatments were assessed using predetermined polynomial contrasts to determine whether differences were a function of P-supply and whether cultivars responded differently to treatments

Spearman Rank Order correlations (R) were used to determine whether the extent of colonization of inoculated plants was related to growth and whether tuber composition in 2002 was related to growth in 2003. All analyses were performed using Statistica® (Statsoft, Inc., Tulsa, Okla., USA, 1996).

Results

Mycorrhizal colonization

Mycorrhizal colonization was higher in 'Majestic Red' than in 'Pot of Gold' after both growing cycles (Figure 1). Plants inoculated in the first growing cycle (2002) were colonized in the second growing cycle (2003) even though plants were not re-inoculated in 2003. In 2003, colonization of both cultivars increased with increased P-rate.

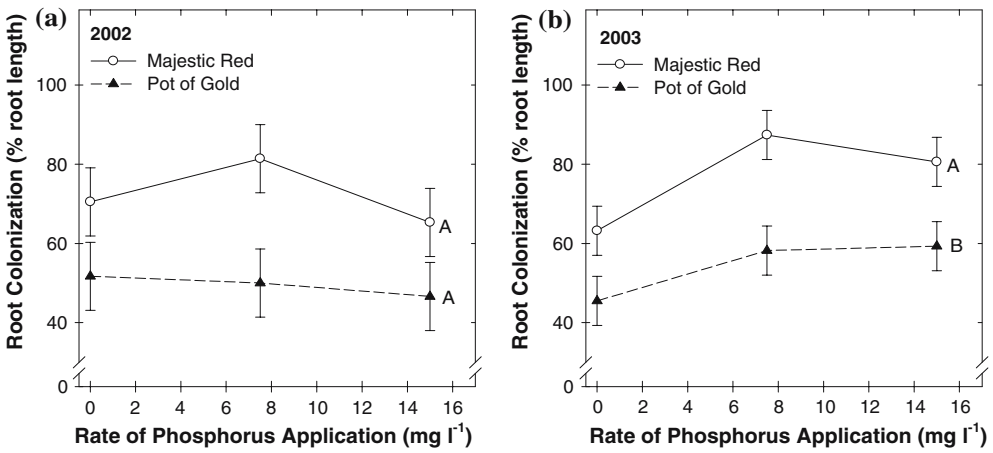


Figure 1. Percentage root colonization of 'Majestic Red' and 'Pot of Gold' calla lily (*Zantedeschia* spp.) grown with inoculum of the arbuscular mycorrhizal fungus, *Glomus intraradices*, and fertilized weekly with 0, 7.5 or 15 mg l^{-1} phosphorus for two growing cycles (a, 2002; b, 2003). Colonization was assessed at the end of each growing cycle. Bars on data points represent 95% confidence intervals based on Bonferroni Test (2002, n = 16; 2003, n = 8). Lines with the same upper case letter beside them within a growing cycle denote similar responses to P-fertilization based on polynomial contrasts ($P = 0.05$).

Vegetative shoot production

Shoot emergence of non-inoculated plants was promoted by increased P-rate (Figure 2a and b). During 2002, inoculation delayed shoot emergence of plants grown at the high P-rate (0.150 mg l^{-1}) by approximately 3–5 d. During 2003, AMF inoculation promoted shoot emergence of both cultivars grown at the low P-rate and 'Majestic Red' at the moderate P-rate. Shoot emergence of inoculated plants in 2003 was negatively correlated with the extent of root colonization in 'Majestic Red' ($R = -0.487$, $P < 0.016$, n = 24) but not 'Pot of Gold'.

'Pot of Gold' produced approximately two more shoots per plant, on average, than 'Majestic Red' (Figure 2c and d). During 2002, the number of shoots on both cultivars increased with increased P-rate, and inoculation only increased shoots on 'Pot of Gold'. In 2003, inoculation increased shoots on both cultivars. In fact, shoot number was positively correlated with the percentage of root length colonized by mycorrhizal fungi for both cultivars during 2003 ('Majestic Red' – $R = 0.434$, $P < 0.034$, n = 24; 'Pot of Gold' – $R = 0.453$, $P < 0.026$, n = 24).

Aboveground vegetative biomass was unaffected by P-rate or inoculation for either cultivar, though 'Pot of Gold' produced more (2002, $P < 0.001$, n = 96; 2003, $P < 0.001$, n = 48) than twice as much as 'Majestic Red' in 2002 (6.9 ± 0.31 g vs. 2.9 ± 0.12 g) and 2003 (7.3 ± 0.43 g vs. 3.4 ± 0.19 g).

Flower production

During 2002, the first flowers on 'Majestic Red' became fully expanded 58–61 DAP or 30–37 d after shoot emergence and the first flowers on 'Pot of Gold' became fully expanded 55–66 DAP or 30–60 d after shoot emergence (Figure 3a and c). P-rate had no influence on the time of flower emergence after planting (Figure 3a) and increased P-rate delayed flower emergence after shoot emergence (Figure 3c). During 2003, increased P-rate delayed flower emergence of 'Majestic Red' and promoted early flower emergence of 'Pot of Gold' (Figure 3b and d). Inoculation had no effect on the time of flower emergence of 'Majestic Red' and promoted early flower emergence of 'Pot of Gold'. In 2003, root colonization was positively correlated with the number of days until shoot ($R = 0.434$, $P < 0.034$, n = 24) and flower emergence ($R = 0.525$, $P < 0.008$, n = 24) in 'Pot of Gold', but not in 'Majestic Red'.

Inoculation delayed peak flowering on 'Majestic Red' by ~4 d, and increased the duration of flower production and maximum number of marketable flowers available on plants (Table 1). By contrast, inoculation promoted earlier peak

flowering of 'Pot of Gold', decreased duration of flower production, and had no influence on the number of marketable flowers produced. Differences in time of peak production of marketable flowers between plants grown at low and high P-rates varied by ~2 d and were delayed by higher rates of P supply (Table 1). Increased P-rate decreased the duration of flower production and the maximum number of flowers produced by plants.

In 2002, inoculation did not influence the total number of flowers produced (Figure 3e) or rate of flower production (Table 1), and promoted flower senescence. In 2003, inoculation increased total number of flowers produced. In 2002, the rate of flower production was greatest on plants grown at the moderate P-rate (7.5 mg l^{-1}) and the rate of flower senescence was greatest at the low P-rate.

Tuber production and composition

Tubers of inoculated 'Majestic Red' had more biomass than tubers of inoculated 'Pot of Gold' in both 2002 and 2003 (Cultivar x AMF treatment interaction: 2002, $P < 0.02$; 2003, $P < 0.004$) (Figure 2e and f). Inoculation increased tuber biomass of 'Majestic Red' in both growing cycles, but only increased tuber biomass of 'Pot of Gold' grown at the low P-rate in 2003. Increased P-rate increased tuber biomass of both cultivars; however, the change in tuber biomass in response to increased P was greater in 'Majestic Red' than in 'Pot of Gold'.

Inoculation increased accumulation (i.e. increased both concentration and content) of N, K, Ca, Fe, Cu, and amino acids in tubers of 'Majestic Red' and decreased accumulation of protein (Tables 2 and 3). In contrast, inoculation increased accumulation of N, P, Cu, and glucose in tubers of 'Pot of Gold' and decreased accumulation of Fe. In tubers from inoculated plants, increasing P-rate increased accumulation of N, P, Ca, S, and glucose and decreased Cu and amino acids. In tubers from un-inoculated plants, increased P-rate decreased Fe and amino acid accumulation. For both cultivars increasing P-rate increased accumulation of N, P, Ca, and glucose and decreased accumulation of amino acids.

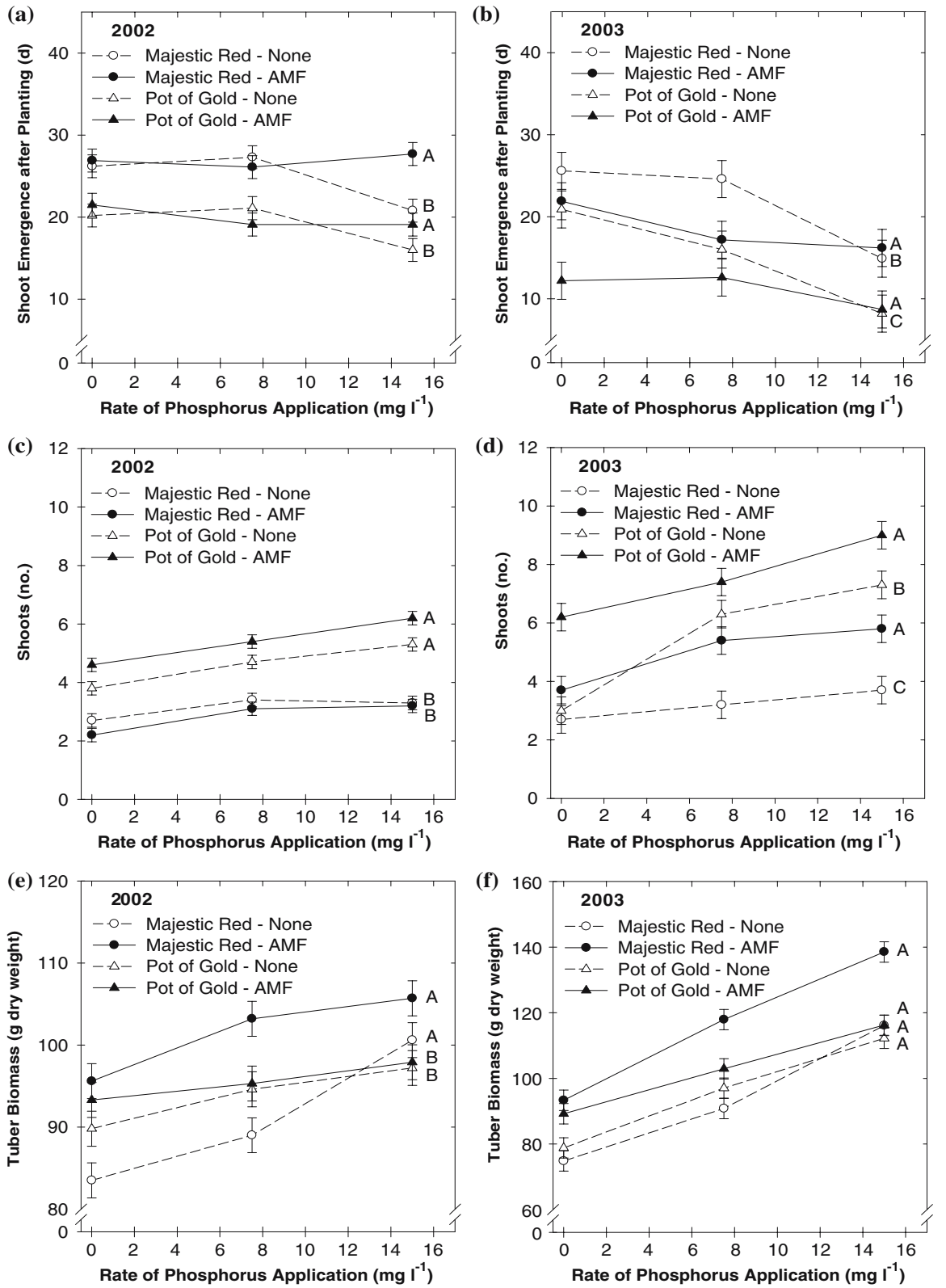
Tubers of 'Majestic Red' contained 0.9–1.3 mg g^{-1} Mg, 0.08–0.11 mg g^{-1} Mn, 0.006–0.011 mg g^{-1} B, and 0.04–0.05 mg g^{-1} Zn while tubers of 'Pot of Gold' contained 1.0–1.4 mg g^{-1} Mg, 0.07–0.10 mg g^{-1} Mn, 0.005–0.008 mg g^{-1} B, and 0.03–0.04 mg g^{-1} Zn. P-rate and AMF-inoculation had no influence on concentrations or contents of Mg, B, Mn or Zn in tubers (data not shown). Tubers of 'Majestic Red' contained approximately 7–18 mg g^{-1} fructose and 2–12 mg g^{-1} sucrose while tubers of 'Pot of Gold' contained 10–26 mg g^{-1} fructose and 4–14 mg g^{-1} sucrose. Sucrose and fructose concentrations in tubers respondedsimilarly to P-rate and inoculation treatments as glucose (data not shown).

Increased concentrations and contents of glucose and starch in tubers in 2002 were correlated with earlier shoot emergence and number of shoots produced in 2003 ($R > 0.52$, $P < 0.01$, $n = 24$). Increased concentrations and contents of P and N in tubers in 2002 were associated with earlier flower emergence in 2003 ($R > 0.57$, $P < 0.01$, $n = 24$). Flower production (number) in 2003 was positively related to K concentrations and content in tubers at the end of 2002 ($R > 0.48$, $P < 0.05$, $n = 24$).

Discussion

We found that inoculation with AMF has organ-specific effects on tuber and flower productivity and quality of calla lily. For example, inoculation increased tubers size regardless of P supply rate, but had variable effects on flowering (time, length, number of flowers, marketable flower, etc.) depending on P-rate and cultivar. The effects of AMF on tuber size were a result of increased nutrient storage in tubers and growth and

Figure 2. Tuber biomass (a, b), time of shoot emergence (c, d) and number of shoots (e, f) of 'Majestic Red' (MR) and 'Pot of Gold' (PG) calla lily (*Zantedeschia* spp.) grown with (AMF) or without (None) inoculum of the arbuscular mycorrhizal fungus (AMF), *Glomus intraradices*, and fertilized with 0, 7.5 or 15 mg l^{-1} phosphorus for two growing cycles (2002, 2003). Bars on data points represent 95% confidence intervals based on Bonferroni's Test (2002, $n = 16$; 2003, $n = 8$). Lines with the same upper case letter beside them denote similar responses to P-fertilization based on polynomial contrasts ($P = 0.05$).


(a)
2002
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Shoot Emergence after Planting (d)
Rate of Phosphorus Application (mg l-1)
A
B
A
B
(b)
2003
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Shoot Emergence after Planting (d)
Rate of Phosphorus Application (mg l-1)
A
B
A
C
(c)
2002
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Shoots (no.)
Rate of Phosphorus Application (mg l-1)
A
A
B
B
(d)
2003
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Shoots (no.)
Rate of Phosphorus Application (mg l-1)
A
B
A
C
(e)
2002
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Tuber Biomass (g dry weight)
Rate of Phosphorus Application (mg l-1)
A
A
B
B
(f)
2003
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Tuber Biomass (g dry weight)
Rate of Phosphorus Application (mg l-1)
A
A
A
A

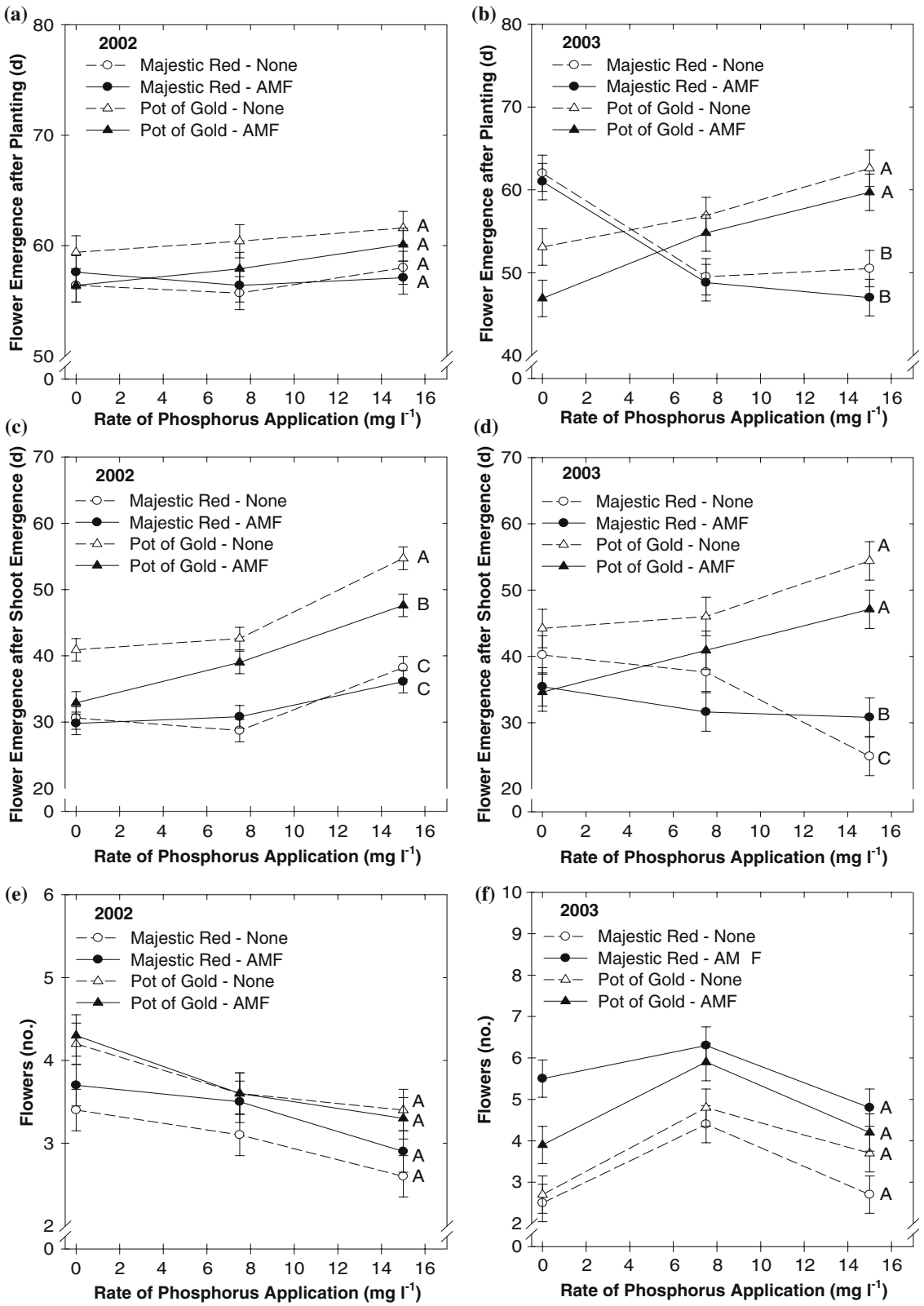

(a)
2002
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Flower Emergence after Planting (d)
Rate of Phosphorus Application (mg l-1)
A
A
A
A
(b)
2003
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Flower Emergence after Planting (d)
Rate of Phosphorus Application (mg l-1)
A
A
B
B
(c)
2002
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Flower Emergence after Shoot Emergence (d)
Rate of Phosphorus Application (mg l-1)
A
B
C
C
(d)
2003
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Flower Emergence after Shoot Emergence (d)
Rate of Phosphorus Application (mg l-1)
A
A
B
C
(e)
2002
Majestic Red - None
Majestic Red - AMF
Pot of Gold - None
Pot of Gold - AMF
Flowers (no.)
Rate of Phosphorus Application (mg l-1)
A
A
A
A
(f)
2003
Majestic Red - None
Majestic Red - AM F
Pot of Gold - None
Pot of Gold - AMF
Flowers (no.)
Rate of Phosphorus Application (mg l-1)
A
A
A
A

Figure 3. Time of flower emergence after planting (a, b) and shoot emergence (c, d) and number of flowers (e, f) of 'Majestic Red' (MR) and 'Pot of Gold' (PG) calla lily (*Zantedeschia* spp.) grown with (AMF) or without (None) inoculum of the arbuscular mycorrhizal fungus (AMF), *Glomus intraradices*, and fertilized with 0, 7.5 or 15 mg l^{-1} phosphorus for two growing cycles (2002, 2003). Bars on data points represent 95% confidence intervals based on Bonferroni's Test (2002, n = 16; 2003, n = 8). Lines with the same upper case letter beside them denote similar responses to P-fertilization based on polynomial contrasts ($P = 0.05$).

resource allocation differences between cultivars. The effects of AMF on flowering were a result of the influence of AMF on shoot development, resource allocation during tuber and floral development, and cultivar variation in response to P supply. We also found that AMF not only influenced calla during the growing cycle in which plants were inoculated, but also influenced plant performance in the growing cycle after inoculation via its effect on tuber quality.

Differences in P-requirements of for flower and tuber production between 'Pot of Gold' and 'Majestic Red' influenced the response of these cultivars to AMF. The P-requirements for aboveground growth of 'Pot of Gold' are greater than 'Majestic Red', and Majestic Red has greater P-requirements for tuber production. This between-cultivar variation in nutritional requirements is common in horticultural crops selected for traits other than nutrient use (Abbey et al., 2002; Alva et al., 2002) and ultimately may regulate differences in cultivar response to AMF (Bryla and Koide, 1998; Poulton et al., 2002).

Increased P-uptake is one of the primary benefits attributed to root colonization by AMF for most crops (Smith and Read, 1997). If aboveground growth of 'Pot of Gold' was truly more sensitive to reduced P-supply than 'Majestic Red', then shoot responses of 'Pot of Gold' to AMF colonization should be greater than 'Majestic Red'. Similarly, if tuber biomass of 'Majestic Red' was more sensitive to reduced P-supply than 'Pot of Gold, then tuber biomass response of 'Majestic Red' to AMF colonization should be greater than 'Pot of Gold'. Indeed, in 2002, inoculation increased shoot production of 'Pot of Gold' but not 'Majestic Red', and tuber biomass of 'Majestic Red' was more responsive to inoculation than 'Pot of Gold'. Hence, our results show that calla responses to AMF are not only a function of P-availability, but also a function of the organ involved. However, we only assessed biomass at the end of the growing cycle, a more complete assessment of AMF and P-effects on differences in organ-specific nutrient requirements between the two cultivars could be determined by performing multiple harvests throughout a growing cycle.

Our results show that organ-specific benefits of AMF-inoculation change over time (growing cycle). For example, AMF had no influence on 'Majestic Red' shoot production (number) in 2002 but increased the number of shoots in 2003. Inoculation altered aspects of tuber quality in 2002 that were associated with increased shoot number in 2003 (e.g. tuber composition). Shoot development in calla is not limited by the number of preformed shoots present at the time of planting and tuber growth is primarily related to the availability of assimilates in excess of the demands of shoot development (Funnell et al., 1998). Differences in the effects of AMF-inoculation between growing cycles may be a result of resource allocation differences between cultivars. For example, 'Pot of Gold' produces a larger canopy than 'Majestic Red', thus requiring more resources. Hence, mycorrhizal benefits to 'Pot of Gold' in 2002 were more obvious in canopy development, while benefits to 'Majestic Red' were more obvious in tuber growth and subsequent enhancement of shoot production (number) in 2003 as a secondary result of increased tuber quality. Responses to AMF-inoculation in other floral geophytes were also greater in the growing cycle after inoculation than the growing cycle in which plants were inoculated (Scagel, 2003a, b; 2004a, b). These types of carry-over effects of AMF are important to consider with perennial crops where growth and development in one growing cycle depends upon plant history from the prior growing cycles and on current growing conditions.

Arbuscular mycorrhizas have been shown to enhance uptake of nutrients other than P (Clark and Zeto, 2000). The ability of AMF to enhance P in tubers without influencing tuber growth for 'Pot of Gold' suggests that AMF inoculation enhanced P uptake, but other nutrients still limited tuber growth. Increasing P supply altered accumulation of nutrients other than P depending on whether plants were inoculated or not.

Table 1. Marketable and total flower production characteristics of 'Majestic Red' and 'Pot of Gold' of calla lily (*Zantedeschia* spp.) grown with (AMF) or without (None) inoculum of the arbuscular mycorrhizal fungus, *Glomus intraradices*, for one growing season (2002) and fertilized with 0, 7.5 or 15 mg l^{-1} phosphorus

Treatment interactions[a]		Marketable flowers[b]			Total flower	
		Maximum (no.)	Duration (d)	Peak (DAP)	Production (no. d^{-1})[c]	Senescence (no. d^{-1})[c]
Cultivar x P-rate						
Majestic Red	0	1.9	28.1	71.8	0.19	0.27
	7.5	2.3	27.4	72.0	0.27	0.21
	15	1.5	25.3	73.7	0.17	0.15
Pot of Gold	0	2.1	39.0	76.2	0.17	0.22
	7.5	2.1	32.8	76.8	0.21	0.20
	15	1.8	29.3	78.6	0.16	0.18
Contrasts	Significance level					
	MR vs. PG (P-response)	ns	**	ns	ns	***
	MR (P-response)	**	*	*	*	**
	PG (P-response)	*	***	*	*	ns
Inoculation x P-rate						
None	0	2.0	35.4	74.3	0.18	0.19
	7.5	1.9	30.4	75.0	0.21	0.18
	15	1.4	28.7	76.4	0.13	0.14
AMF	0	2.3	34.3	74.8	0.18	0.31
	7.5	2.4	31.8	75.3	0.21	0.20
	15	1.8	28.5	77.9	0.16	0.18
Contrasts	Significance level					
	None vs. AMF (P-response)	ns	ns	ns	ns	**
	None (P-response)	**	**	*	**	*
	AMF (P-response)	*	**	*	*	***
Cultivar x inoculation						
Majestic Red	None	1.7	24.8	70.6	0.20	0.18
	AMF	2.2	29.2	74.5	0.21	0.23
Pot of Gold	None	1.9	38.3	79.9	0.15	0.16
	AMF	2.1	34.0	77.6	0.15	0.24
Contrasts	Significance level					
	MR vs. PG (None vs. AMF)	*	***	***	ns	ns
	MR (None vs. AMF)	**	**	**	ns	**
	PG (None vs. AMF)	ns	**	*	ns	**

[a]Means from treatment interactions and P-values for polynomial contrasts (*** < 0.001, ** < 0.01, * < 0.05, ns > 0.05) comparing responses to treatments.
[b]From fitted log-normal equations of data collected daily on marketable flowers per plant. Max. = maximum marketable flowers per plant; Duration = the length of time marketable flowers are available on plants; Peak = time of peak flowering after planting.
[c]From fitted logistic equations of data collected daily on total number of flowers per plant. Production = rate of flowers produced between when plants produced 1 flower and the maximum number of flowers produced. Senescence = rate of flower senescence between when flowers started to senesce and the end of the experiment.

For example, inoculation increased allocation of N and Cu to tubers at the low P-rate and N, P, K, S, and Ca at the high P-rate. Depending on the P-rate, tuber growth was limited by different nutrients and thus the influence of AMF on the accumulation of nutrients other than P varied with P-rate. Charron et al. (2001), showed that inoculation of onion with AMF increased accumulation of N, P, K, Ca, Mg, Fe, Mn, and Zn in bulbs even though increased P supply only increased accumulation of P, Fe, and Mn. Inoculation of other geophyte floral crops with AMF can increase accumulation of N, K, S, Ca, and Zn in corms without any increase in P accumula-

Table 2. Concentration and content of nutrients in 'Majestic Red' (MR) and 'Pot of Gold' calla lily (*Zantedeschia* spp.) tubers grown with (AMF) or without (None) inoculum of the arbuscular mycorrhizal fungus, *Glomus intraradices*, for one growing cycle (2002) and fertilized with 0, 7.5 or 15 mg l^{-1} phosphorus

Treatment interactions[a]		Nitrogen		Phospho-rus		Potassium		Calcium		Sulfur		Iron		Copper	
		mg g^{-1}	mg	mg g^{-1}	mg	mg g^{-1}	mg	mg g^{-1}	mg	mg g^{-1}	mg	μg g^{-1}	mg	μg g^{-1}	mg
Cultivar x P-rate															
Majestic Red	0	10.3	921	1.46	130	9.5	850	7.75	690	1.14	101	592	52.7	7.5	0.69
	7.5	10.1	958	1.65	155	10.1	956	7.46	701	1.12	106	520	49.3	5.5	0.51
	15	11.6	1163	1.71	173	10.7	1075	8.41	849	1.20	121	504	50.6	5.0	0.50
Pot of Gold	0	4.8	480	1.5	137	11.0	1007	5.78	594	0.97	89	532	48.3	5.0	0.45
	7.5	5.3	500	1.49	154	10.7	1109	6.70	608	1.07	111	441	44.7	4.5	0.67
	15	5.7	578	1.65	170	9.7	984	6.94	705	1.09	112	446	45.2	5.6	0.56
Contrasts	Significance level														
	MR vs. PG (P-response)	ns	ns	ns	ns	***	*	ns	ns	*	ns	ns	ns	***	***
	MR (P-response)	***	**	***	***	***	**	*	***	ns	*	**	ns	***	***
	PG (P-response)	*	*	*	**	***	ns	*	*	*	*	**	ns	ns	***
Inoculation x P-rate															
None	0	6.9	622	1.44	128	9.8	878	6.55	606	1.07	95	597	53.0	5.7	0.506
	7.5	7.0	631	1.49	139	10.0	945	7.30	647	1.12	106	469	43.8	4.4	0.406
	15	7.2	727	1.52	151	9.4	933	7.24	717	1.05	104	448	44.1	5.5	0.538
AMF	0	8.0	778	1.52	140	10.6	978	6.69	650	1.04	95	527	47.9	7.0	0.633
	7.5	8.5	827	1.65	170	10.8	1120	7.15	689	1.07	112	493	50.2	5.6	0.577
	1	10.0	1014	1.84	192	10.9	1126	8.11	837	1.24	129	501	51.7	5.1	0.530
Contrasts	Significance level														
	None vs. AMF (P-response)	*	*	*	ns	*	ns	*	*	**	*	**	***	**	**
	None (P-response)	ns	*	ns	*	*	*	ns	ns	ns	ns	***	**	ns	ns
	AMF (P-response)	***	***	***	***	ns	*	**	***	***	***	ns	ns	***	**
Cultivar x inoculation															
Majestic Red	None	9.3	874	1.57	146	9.2	861	7.43	697	1.13	106	471	43.9	5.7	0.526
	AMF	12.0	1154	1.65	159	11.0	1060	8.32	797	1.17	113	606	57.8	6.5	0.611
Pot of Gold	None	4.8	446	1.40	132	10.4	977	6.62	617	1.03	97	538	50.0	4.7	0.440
	AMF	5.7	593	1.69	176	10.5	1089	6.32	654	1.06	111	408	42.1	5.3	0.549
Contrasts	Significance level														
	MR vs. PG (None vs. AMF)	***	ns	*	*	***	ns	***	ns	ns	ns	***	***	ns	ns
	MR (None vs. AMF)	**	***	ns	ns	***	***	***	**	ns	ns	***	***	*	**
	PG (None vs. AMF)	***	***	***	***	ns	*	ns	*	ns	ns	***	***	*	***

[a]Means from treatment interactions and P-values for polynomial contrasts (*** < 0.001, ** < 0.01, * < 0.05, ns > 0.05) comparing responses to treatments.

tion (Scagel, 2003a; 2004a, b). Plant responsiveness to AMF-colonization is obviously a result of a complex interaction between P-supply and the availability of other essential nutrients (Valentine et al., 2001). Differential responses in nutrient accumulation associated with P supply and AMF of calla indicate that complex interactions occur between nutrients and emphasize the importance of looking at nutrients other than just P when assessing responses to AMF.

Differences in resource allocation (biomass) between modes of reproduction in geophytes are related to flowering demands of different genotypes, but are not considered a response to

Table 3. Concentration and content of protein, amino acids, glucose, and starch in 'Majestic Red' and 'Pot of Gold' calla lily (*Zantedeschia* spp.) tubers grown with (AMF) or without (None) inoculum of the arbuscular mycorrhizal fungus, *Glomus intraradices*, for one growing cycle (2002) and fertilized with 0, 7.5 or 15 mg l^{-1} phosphorus

Treatment interactions[a]		Protein[b]		Amino acids		Glucose		Starch[b]	
		mg g^{-1}	g	mg g^{-1}	mg	mg g^{-1}	mg	mg g^{-1}	mg
Cultivar x P-rate									
Majestic Red	0	46.5	4.01	3.11	269	1.38	120	47.5	4.13
	7.5	43.1	4.14	2.49	241	1.91	157	48.1	4.59
	15	42.1	4.13	2.23	221	1.93	195	46.8	4.57
Pot of Gold	0	45.2	4.19	3.10	287	1.92	180	50.8	4.72
	7.5	39.4	3.54	2.72	245	2.44	221	57.9	5.22
	15	44.2	4.27	2.14	208	2.66	259	61.1	5.95
Contrasts	Significance level								
	MR vs. PG (P-response)	*	ns	ns	ns	ns	ns	***	*
	MR (P-response)	*	ns	**	*	**	**	ns	ns
	PG (P-response)	ns	ns	***	***	***	**	***	**
Inoculation x P-rate									
None	0	50.0	4.28	2.64	232	1.59	138	49.5	4.27
	7.5	45.9	4.29	2.17	202	1.93	182	54.3	5.07
	15	44.1	4.27	1.97	191	1.87	184	57.0	5.54
AMF	0	41.9	3.92	3.45	324	1.72	161	59.7	4.57
	7.5	36.6	3.39	3.05	283	2.11	196	50.7	4.74
	15	42.2	4.12	2.41	238	2.72	269	51.0	4.98
Contrasts	Significance level								
	None vs. AMF (P-response)	*	ns	ns	ns	**	*	*	*
	None (P-response)	*	ns	**	*	ns	ns	***	***
	AMF (P-response)	Ns	ns	***	***	***	***	ns	ns
Cultivar x inoculation									
Majestic Red	None	50.3	4.46	2.08	183	1.57	142	51.8	4.63
	AMF	37.5	3.72	3.07	303	1.70	173	42.5	4.22
Pot of Gold	None	42.9	4.10	2.45	234	2.02	195	55.4	5.29
	AMF	42.7	3.89	2.87	259	2.66	245	57.8	5.31
Contrasts	Significance level								
	MR vs. PG (None vs. AMF)	***	*	*	***	*	*	***	ns
	MR (None vs. AMF)	***	**	***	***	ns	ns	***	ns
	PG (None vs. AMF)	ns	ns	*	ns	***	*	ns	ns

[a]Means from treatment interactions and P-values for polynomial contrasts (*** < 0.001, ** < 0.01, * < 0.05, ns > 0.05) comparing responses to treatments.
[b]Protein and starch data expressed as amino acids from protein and glucose equivalents from starch, respectively.

nutrient availability (Ronsheim and Bever, 2000). Our prior work with floral geophytes showed that colonization of plants by AMF can alter partitioning of biomass between different plant parts (Scagel 2003a; 2004a, b). With calla, AMF can increase tuber biomass; however, the benefits derived from inoculation vary with nutrient availability, nutrient demands of the plant, and resource allocation patterns during plant development. With calla, tuber growth is initiated between 38 and 65 d after planting and growth rate and time of initiation is primarily related to the availability of assimilates in excess of the demands of shoot and flower development (Funnell et al. 2002). Greatest rates of nutrient uptake by calla occurs between 42 and 84 DAP in field-grown plants (Clark and Boldingh, 1991), which suggests that demands from shoot, flower, and tuber development are highest during this time. We found both P supply and AMF inoculation increased

tuber biomass of 'Majestic Red' in both growing cycles, while AMF had little effect on tuber biomass of 'Pot of Gold'. Since 'Majestic Red' produced a smaller canopy and fewer flowers than 'Pot of Gold', more resources were potentially available for allocation to tubers. The response 'Majestic Red' tuber biomass to AMF and P-supply is similar to the yield responses reported for *Allium* spp. (Al-Karaki, 2002; Charron et al., 2001).

We assessed differences in resource allocation to tubers between 'Majestic Red' and 'Pot of Gold' in response to AMF and P supply by measuring the accumulation or storage of certain organic constituents in tubers. Organic sources of C and N stored in tubers at the end of a growing cycle are important for growth during the following growing cycle (Funnell et al., 1998). Inoculation and increased P supply increased accumulation of starch and reducing sugars in tubers of 'Pot of Gold'. In contrast, inoculation only increased accumulation of amino acids in 'Majestic Red' and had no influence on starch or reducing sugars. The influence of AMF on resource allocation to tubers of 'Pot of Gold' is a function of P supply while the influence of AMF on resource allocation to tubers of 'Majestic Red' does not appear to be related to P supply. Inoculation of Freesia and harlequin flower with AMF increased protein, amino acid, and reducing sugars in corms when plants were grown at P-rates similar to the moderate P-rate (7.5 mg l^{-1} P) used in this experiment (Scagel, 2003a; 2004a).

Prior to leaf area development, growth of calla is primarily a function of stored reserves in the tuber (Funnell et al., 2002) and initial growth could be delayed by resource demands of establishing mycorrhizal symbiosis. AMF-inoculation causes no delay in shoot emergence during the initial stages of plant growth after inoculation of several different floral geophytes (Scagel, 2004a; 2003a, b). With calla, we found that that low P in tubers and inoculation with AMF can delay shoot development during the initial establishment of the symbiosis; however, AMF-inoculation altered aspects of tuber quality (e.g. tuber composition) that enhanced shoot development in the growing cycle following inoculation. Similar effects of AMF-inoculation on the time of shoot emergence of wild hyacinth (Scagel, 2004b) and Easter lily (*Lillium longiflorumm*) (Mora, 1990) have been reported.

AMF have been shown to preferentially alter allocation to the symbiosis over flowering (Korhonen et al., 2004) and enhance early flowering (Sohn et al., 2003); however, flower initiation and development in the species used in these studies occurs during the growing cycle in which the plant produces flowers. With calla, flower buds are pre-formed prior to planting (Funnell, 1993) and floral differential occurs under conditions suitable for vegetative development (Funnell et al., 2002); therefore we hypothesized that AMF-inoculation would have little influence on flowering of calla during the first growing cycle after inoculation. Our results show that initial demands of establishing the symbiotic association between calla and *G. intraradices* does not negatively influence flowering. In fact, on average, inoculated plants produced more flowers during both growing cycles of our study. Typically, flowers are not completely differentiated at planting; therefore, the potential for flowering exists as long as vegetative development continues (Corr and Widmer, 1990). Colonization of calla by AMF influences flower differentiation after flower bud formation and alters aspects of tuber quality that affects flowering in the following growing cycle. Similar effects of AMF-inoculation flowering responses of Easter lily (Mora, 1990) and wild hyacinth (Scagel, 2004b) have been reported.

Flowering of calla can be enhanced by increasing P in irrigation solution (Gracia-Garza et al. 2004). Interestingly, we found that flower production of both cultivars in 2002 was slightly enhanced by lower P rates. Decreased flower production at higher P rates may initially seem counter-intuitive since, in general, better fertility increases production and P is known for its importance in flowering. However, geophytes like calla have two reproductive strategies in response to changing resources and environments – sexual (flowering) and vegetative (tuber). In natural habitats, different advantages may exist for producing sexual vs. asexual progeny, as sexual progeny may be favored in the presence of pathogen or changing environments and asexual progeny may be favored in static environments (Loehle, 1987; Rohsheim and Bever, 2000). With calla, these multiple reproductive strategies influences plant response to different P levels and responsiveness to AMF. Although AMF have been shown to increase reproduction (via both

male and female functions) in several plant species (Koide and Dickie, 2002), our results suggest that plant responses to AMF in terms of reproduction may vary depending on the reproductive strategy of the plant as well as response to other environmental factors (e.g. P).

Mycorrhizal inoculation of calla increased the number of flowers produced by plants and enhanced other factors important to commercial production of calla, including number of marketable flowers produced, flower production rate, and duration of flower production. We found with 'Majestic Red' that the rate of flower senescence was also increased by inoculation. In contrast, data from Gaur et al. (2000) shows that AMF inoculation of petunia (*Petunia x hybrida*), Chinese aster (*Callistephus chinensis*), and spotted snapweed (*Impatiens balsamina*) increased flower production, but had no influence on flower senescence. This difference in flower senescence in response to AMF between calla and the species used by Gaur et al. (2000) may be a result of differences in allocation patterns between annuals and perennials in response to AMF-inoculation.

Our results show that although calla response to AMF depends on cultivar and P supply, the benefits of AMF to growers depend on their specific crop product. For example, inoculation of 'Majestic Red' increases tuber biomass regardless of P-supply; however, AMF influence on marketable flower production was depends on P-supply. Even though AMF increased the maximum number of marketable flowers produced, inoculation delayed peak time of production, lengthened time of flowering, and promoted flower senescence. For 'Majestic Red', benefits from inoculation with *G. intraradices* were primarily on tuber yield, and effects on flowering could be considered negative for growers of calla for potted and cut flowers. For 'Pot of Gold', AMF-enhanced shoot production was similar to the response of this cultivar to increased P-supply. However, AMF also improved bulb quality in the first growing cycle resulting in increased tuber biomass and flower production in the following growing cycle. This later effect was not directly a result of improved P nutrition.

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