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Nutritional, growth, and reproductive responses of maize (*Zea mays* L.) to arbuscular mycorrhizal inoculation during and after drought stress at tasselling

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Abstract The effects of root colonization by the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* Schenck & Smith on nutritional, growth, and reproductive attributes of two tropical maize cultivars with different sensitivities to drought were studied. Freshly regenerated seeds of selection cycles 0 (cv. C0, drought-sensitive) and 8 (cv. C8, drought-resistant) of the lowland tropical maize population “Tuxpeño sequía” were used in this greenhouse experiment. Maize plants were subjected to drought stress for 3 weeks following tasselling (75–95 days after sowing) and rewatered for the subsequent 5 weeks until harvest. Mycorrhizal (M+) plants had significantly higher uptake of N, P, K, Mg, Mn, and Zn into grain than non-mycorrhizal (M–) plants under drought conditions. AM inoculation also produced significantly greater shoot masses in C0 and C8 regardless of the drought-stress treatment. In the sensitive cultivar C0, drought stress reduced the shoot mass and grain yield by 23% and 55%, respectively, when roots were not colonized, while the reductions were only 12% and 31%, respectively, with mycorrhizal association. In addition, the emergence of tassels and silks was earlier in M+ plants than in M– plants under drought conditions. Mycorrhizal response was more pronounced under both well-watered and drought conditions in C0 than in the C8 cultivar. The overall results suggest that AM inoculation affects host plant nutritional status and growth and thereby alters the reproductive behaviour of maize under drought conditions.

Key words Arbuscular mycorrhizae · Drought · Grain yield · Maize · Nutrition

Introduction

In maize, grain yield reduction caused by drought ranges from 10% to 76% depending on the severity and stage of occurrence (Bolaños et al. 1993). Drought stress coinciding with flowering delayed silking and resulted in an increase in the anthesis-silking interval (Bolaños and Edmeades 1993a); this was usually associated with reductions in grain number and yield (Edmeades et al. 1993). Bolaños and Edmeades (1993b) observed a negative exponential relationship between grain yield and ASI when the tropical maize population “Tuxpeño sequía” was subjected to drought at flowering; grain yield declined by 90% as ASI increased from 0 to 10 days. Westgate (1994) reported that water deficit after anthesis shortened the duration of grainfilling by causing premature desiccation of the endosperm and by limiting embryo volume. More recently, Zinselmeier et al. (1995) showed an increase in the frequency of zygotic abortion in maize exposed to drought during pollination which could completely eliminate kernel set and result in considerable yield loss.

The arbuscular mycorrhizal fungi form symbiotic associations with nearly all agricultural plants. These fungi have attracted the interest of soil and plant scientists from the perspectives of plant nutrition (McArthur and Knowles 1993; Medeiros et al. 1994; Tobar et al. 1994a, b), drought (Augé et al. 1994; Subramanian et al. 1995), chilling (Charest et al. 1993; Paradis et al. 1995), alleviation of heavy metal toxicity (Weissenhorn et al. 1995), and biological control of root pathogens (Benhamou et al. 1994; Linderman 1994). Colonization of roots by AM fungi has been shown to improve productivity of several field crops, including maize (Sylvia et al. 1993; Shen et al. 1994), sorghum (Raju et al. 1990), soybean (Bethlenfalvay et al. 1988), and potato (McArthur and Knowles 1993). The responses to AM fungi have been attributed mainly to enhanced uptake and translocation of the slowly diffusing nutrient ions PO_4^- , NH_4^+ , Zn^{2+} , and Cu^{2+} (Nelsen 1987; Kothari et al. 1990; Frey and Schüepp 1993; Tobar et al. 1994b). The external hyphae

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of AM fungi play a vital role, especially in host plant P nutrition, by exploration of a soil volume extending beyond the depletion zone around the roots and by providing access to P, which is otherwise only transported by slow diffusion processes (Jackobsen 1992). However, AM fungi may not significantly contribute to plant growth in soils of high fertility (Jeffries 1987). The degree of AM fungi response increases with decreasing soil fertility (Jeffries 1987) and with increasing intensity of drought stress (Sylvia et al. 1993). Thus AM fungi, as an important factor in nutrient acquisition, may improve drought resistance under suboptimal plant growth conditions (Morgan et al. 1994).

Under drought conditions, mycorrhizal colonization promotes water relations of the host plants through stimulated plant nutrition (an indirect effect) and possibly through enhanced direct water uptake (Allen 1982; Faber et al. 1991). Nelsen (1987) reported that drought tolerance of mycorrhizal onion plants was mainly due to improved P nutrition which contributed to the healthy state of the host plant. Hardie and Leyton (1981) stressed that drought may be relieved by an increased rate of root growth and more efficient extraction of water from the soil as a consequence of increased P uptake. Greater P uptake promoted root growth, which in turn enhanced the hydraulic conductivity and transpiration rate in AM soybean plants (Bethlenfalvay et al. 1988). Augé et al. (1994) obtained AM and non-AM maize plants of comparable size and biomass when the latter received a greater application of inorganic P fertilizer under moderate drought conditions. As with P, the external hyphae of AM fungi also enhanced the uptake of ^{15}N from soil and its transport to host plants (Frey and Schüepp 1993). Under drought conditions, when root NO_3^- uptake was limited by impaired mass flow of the soil solution, Tobar et al. (1994a, b) found that NO_3^- transport through AM hyphae from the soil to lettuce plants resulted in enhanced shoot mass and N uptake in AM plants. AM inoculation has also been shown to enhance uptake of K and Mg (Hall et al. 1977; Hall 1978; Azcón and Ocampo 1981), Ca (Pai et al. 1994), and Cu and Mn (Sylvia et al. 1993), and this may indirectly have an impact on drought resistance of the host plant. Allen (1982) suggested that AM hyphae absorb and translocate water directly to their hosts, thus acting as a bridge between the dry zone around the roots and adjacent moist regions. Kothari et al. (1990) showed that rates of water uptake per unit root length and per unit time by AM maize plants were about twice that of non-AM plants and attributed this to hyphal transport. However, Graham et al. (1987) showed that improvement of water relations of AM citrus plants under drought conditions was unlikely, due to the greater C cost and reduced hydraulic conductivity of mycorrhizal plants.

We hypothesized that inoculation of maize with AM fungi would improve the host plant nutritional status and thus plant growth, which may alter the reproductive behaviour and yield of maize cultivars sensitive to

drought. To test this, we determined the effects on nutrient uptake, shoot mass, grain yield, days to anthesis and days to silking in mycorrhizal and non-mycorrhizal plants of drought-sensitive (C0) and -resistant (C8) maize cultivars exposed to 3 weeks of withheld irrigation following tasselling.

Materials and methods

Plant growth conditions

A greenhouse experiment was conducted at the Central Experimental Farm, Ottawa, using freshly regenerated maize (*Zea mays* L.) seeds of selection cycles 0 (cv. C0, drought-sensitive) and 8 (cv. C8, drought-resistant) of "Tuxpeño sequía" obtained from CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo), Mexico. A $2 \times 2 \times 2$ factorial randomized block design included two cultivars (C0 and C8), two moisture levels [irrigation once each week throughout the crop period (S-) and irrigation withheld for 3 weeks (S+) following tasselling (75–95 days after sowing)], and with AM, *Glomus intraradices* Schenck & Smith; specimen DAOM 181602 (M+) or without AM (M-) inoculation. The details of growth conditions and treatments were presented previously (Subramanian and Charest 1995; Subramanian et al. 1995). At the beginning of the experiment, six maize plants were grown in vermiculite in plastic containers ($65 \times 40.6 \times 42$ cm) with bottom holes. Two plants per container remained at the time of the imposition of the drought stress; the other four plants were used for the root colonization studies. The plants were irrigated once a week depending on the cumulative evapotranspiration rate which was determined gravimetrically. All the plants were fertilized uniformly with 500 ml Hoagland solution per pot per week (N 210 mg; P 31 mg; K 235 mg; Ca 160 mg; Mg 49 mg; S 64 mg; Mn 0.5 mg; Cu 0.02 mg; Zn 0.05 mg; B 0.5 mg; Mo 0.01 mg; and Fe chelate 110 mg, in 1000 ml distilled H_2O) diluted in irrigation water. For the drought treatment, irrigation was withheld for 3 weeks following tasselling (75–95 days after sowing) and then continued for 5 weeks until harvest.

Nutrient analysis

Shoots (after 3 weeks' drought stress and at harvest) and grains were sampled for nutrient analysis. Tissues were dried at 70°C , weighed, and digested in a sealed chamber method (Anderson and Henderson 1986). Briefly, 200 mg of powdered tissue was placed into a glass centrifuge tube, 1–2 ml of a 7:3 (v:v) mixture of HClO_3 and H_2O_2 was added and the tube was tightly capped. After 2 h predigestion at ambient temperature, 1 ml of H_2O_2 was added and the tube was again tightly sealed and placed under the fumehood on a hot plate for 30 min. The digested samples were diluted to 25 ml with distilled H_2O . All the minerals except nitrogen were determined with an inductively coupled argon plasma spectrophotometer (Model 9000, Thermal Jarrel Ash, Waltham, Mass., USA). The N content was estimated (Sivasankar and Oaks 1995) using an Elemental Analyzer (Model NA 1500, Carlo Erba, Milan, Italy). In this paper, the term "nutrient content" refers to the total quantity of nutrients present in the shoot mass.

Shoot mass, grain yield, and harvest index

At the end of 3 weeks' drought stress and at harvest, shoots (stem, leaves, and tassel) and grains were dried at 70°C for 48 h. The ratio of grain yield to shoot mass is termed harvest index (HI). Mycorrhizal dependency (MD) or response to mycorrhizal colonization was calculated using the following formula (Plenchette et al. 1983):

Table 1 Means (n=3) and standard errors (in parentheses) for nutrient content (mg/plant) in shoots of drought-sensitive and -resistant maize cultivars after 21 days in drought-stressed or well-watered conditions with (M+) or without (M-) arbuscular my-

corrhizal colonization. Different letters within a column indicate significant differences ($P \leq 0.05$) using the Tukey's Studentized Range (HSD) test

	N	P	K	Ca	Mg	S	Fe	Mn	Cu	Zn
<i>Drought-sensitive (C0) cultivar</i>										
Drought-stressed										
M+	3437 ^{cd} (119)	709 ^{ab} (77)	4589 ^{bc} (457)	2830 ^{ab} (232)	1203 ^a (68.1)	315 ^a (9.0)	62.1 ^b (2.8)	17.5 ^{ab} (0.6)	2.43 ^b (0.12)	307 ^{abc} (40.6)
M-	2649 ^f (268)	492 ^b (9.9)	3507 ^c (644)	1795 ^c (271)	953 ^a (140)	302 ^a (45.3)	58.7 ^b (4.7)	12.7 ^d (1.4)	1.83 ^c (0.24)	184 ^c (33.5)
Well-watered										
M+	4435 ^{bc} (89)	964 ^a (62)	6162 ^{ab} (539)	3523 ^a (161)	1397 ^a (114)	406 ^a (71.7)	54.8 ^b (3.9)	20.6 ^{ab} (2.6)	3.59 ^a (0.23)	420 ^a (40.5)
M-	3954 ^{cd} (43)	647 ^{ab} (56.8)	5223 ^{abc} (247)	3150 ^{ab} (282)	1250 ^a (145)	315 ^a (28.3)	90.0 ^{ab} (15.5)	14.0 ^{cd} (0.5)	1.86 ^c (0.04)	243 ^{bc} (12.8)
<i>Drought-resistant (C8) cultivar</i>										
Drought-stressed										
M+	4875 ^{ab} (127)	967 ^a (129)	5732 ^{ab} (272)	2904 ^{ab} (147)	1338 ^a (12.5)	365 ^a (42.3)	62.4 ^b (6.4)	22.6 ^a (0.5)	2.71 ^b (0.23)	306 ^{abc} (32.2)
M-	3038 ^{ef} (192)	736 ^{ab} (102)	4089 ^{bc} (232)	2154 ^c (187)	1343 ^a (253)	310 ^a (21.9)	147 ^a (20.4)	20.4 ^{ab} (1.4)	1.91 ^c (0.19)	310 ^{abc} (38.2)
Well-watered										
M+	5571 ^a (199)	1194 ^a (338)	6414 ^{ab} (359)	3572 ^a (415)	1242 ^a (160)	367 ^a (35.4)	66.9 ^b (8.8)	25.8 ^a (0.6)	2.60 ^b (0.05)	339 ^{ab} (25.9)
M-	4889 ^{ab} (210)	778 ^{ab} (47)	7197 ^a (768)	4113 ^a (182)	1204 ^a (75.6)	376 ^a (43.1)	144 ^a (26.7)	19.3 ^{ab} (2.0)	2.67 ^b (0.23)	395 ^{ab} (36.1)
ANOVA: C (cultivars), S (drought treatment), M (mycorrhizal treatment)										
C	***	*	**	*	NS	NS	**	**	**	*
S	***	**	***	***	NS	NS	NS	NS	***	**
M	***	**	**	*	NS	NS	***	*	**	*
C X S	NS	NS	NS	NS	NS	NS	NS	**	*	NS
C X M	*	NS	NS	NS	NS	NS	**	**	NS	**
S X M	**	NS	*	**	NS	NS	NS	NS	NS	NS
C X S X M	*	NS	NS	NS	NS	NS	*	*	*	NS

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.001$ NS not significant

$$\text{MD (\%)} = \frac{\text{Grain yield (M+)} - \text{Grain yield (M-)}}{\text{Grain yield (M+)}} \times 100$$

Reproductive behaviour

During the 3 weeks' drought stress, the day of emergence of male (tasselling) and female (silking) inflorescences was noted. A plant was considered to have flowered or silked if at least one extruded anther or one strand of silk was visible. The difference in days between anthesis and silking is referred to as anthesis-silking interval, ASI (Edmeades et al. 1993).

Statistical analysis

A three-way analysis of variance (ANOVA) was applied (SAS Institute 1989) to all the data, which was also examined using Tukey's Studentized Range (HSD) test.

Results

Nutrient content

The drought treatment at tasselling significantly decreased uptake of N, P, K, Ca, and Cu by the shoots of

M- and M+ plants of C0 and C8 (Table 1). However, drought-stressed M+ plants of C0 had significantly higher contents of N, Ca, Mn, and Cu than M- plants (Table 1). The increases in mineral concentration due to AM colonization in C8 in drought conditions were significant for N, Ca, and Cu and there was a significant decrease in Fe. Regardless of drought treatment, Fe uptake significantly decreased in M+ plants of C8.

Even after 5 weeks' recovery, drought had a significant negative effect on shoot nutrient content (Table 2). Mycorrhizae had a significant effect by increasing nutrient content, except for Cu and Zn. During this period of recovery, AM fungi significantly increased the shoot contents of N, Cu, and Zn in C0, and N, P, and S in C8.

Cultivar, drought treatment, and mycorrhizal colonization had significant effects on the grain contents of most of the minerals examined (Table 3). The drought treatment in general lowered the grain nutrient contents of both M+ and M- plants. However, in drought conditions, significantly higher grain nutrient contents were found in M+ than in M- plants for N, Mg, and Mn in C0, and for N, P, K, Mn, and Zn in C8.

Table 2 Means ($n=3$) and standard errors (in parentheses) for nutrient content (mg/plant) in shoots of drought-sensitive and -resistant maize cultivars at the harvest stage after drought-stressed or well-watered conditions with (M+) or without (M-) arbuscular mycorrhizal colonization. Different letters within a column indicate significant differences ($P \leq 0.05$) using the Tukey's Studentized Range (HSD) test

	N	P	K	Ca	Mg	S	Fe	Mn	Cu	Zn
<i>Drought-sensitive (C0) cultivar</i>										
Drought-stressed										
M+	4340 ^{bc} (315)	803 ^{ab} (38)	5476 ^{ab} (295)	1840 ^{cd} (137)	1735 ^{ab} (215)	383 ^b (100)	129 ^b (21)	27.1 ^b (4.8)	3.18 ^b (0.25)	152 ^b (11)
M-	3085 ^d (152)	633 ^{ab} (107)	3584 ^b (877)	1354 ^d (159)	1496 ^b (83)	364 ^b (25)	127 ^b (3)	27.6 ^b (2.2)	2.47 ^c (0.20)	55.9 ^c (8.1)
Well-watered										
M+	5578 ^{ab} (418)	910 ^a (54)	6563 ^a (895)	3763 ^{abc} (831)	1250 ^a (45)	572 ^{ab} (14)	228 ^a (4)	46.0 ^a (2.8)	4.19 ^{bc} (0.62)	363 ^a (48)
M-	4995 ^{ab} (381)	882 ^a (63)	5678 ^{ab} (1087)	2147 ^{bcd} (349)	1871 ^{ab} (166)	491 ^{ab} (67)	119 ^b (9)	41.5 ^{ab} (4.8)	4.97 ^a (0.52)	180 ^b (18)
<i>Drought-resistant (C8) cultivar</i>										
Drought-stressed										
M+	4547 ^{bc} (255)	892 ^a (100)	5978 ^{ab} (429)	2772 ^{a-d} (528)	1876 ^a (64)	642 ^a (17)	110 ^b (12)	31.5 ^{ab} (3.9)	2.75 ^{bc} (0.10)	54.5 ^c (7)
M-	3223 ^d (212)	489 ^b (78)	5052 ^{ab} (136)	1543 ^d (140)	1734 ^{ab} (73)	343 ^b (15)	232 ^a (14)	26.6 ^b (1.9)	2.50 ^{bc} (0.09)	47.5 ^c (6.6)
Well-watered										
M+	5944 ^a (287)	889 ^a (67)	7735 ^a (786)	4509 ^a (393)	2270 ^a (58)	563 ^{ab} (23.1)	242 ^a (14)	40.1 ^{ab} (3.1)	3.50 ^{abc} (0.22)	157 ^b (15)
M-	4002 ^{bc} (218)	748 ^{ab} (56)	6567 ^a (538)	4219 ^{ab} (626)	2050 ^a (127)	529 ^{ab} (25)	141 ^b (18)	30.1 ^{ab} (1.7)	2.94 ^{bc} (0.31)	456 ^a (18)
ANOVA: C (cultivar), S (drought treatment), M (mycorrhizal treatment)										
C	NS	NS	*	**	*	*	**	NS	**	*
S	***	***	***	***	***	**	**	***	***	***
M	***	*	**	**	**	**	*	*	NS	NS
C X S	NS	NS	NS	NS	NS	NS	NS	*	*	**
C X M	NS	*	NS	NS	NS	NS	**	NS	NS	***
S X M	NS	NS	NS	NS	NS	NS	***	NS	NS	**
C X S X M	NS	NS	NS	NS	NS	*	**	NS	NS	***

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.001$ NS not significant

Shoot mass

Shoot mass measured after 3 weeks of drought stress following tasselling was significantly higher in M+ than in M- plants of C0 (Fig. 1, Table 4). Drought stress reduced the shoot mass of M- C0 plants by 23% but only by 12% in M+ plants. A similar trend was also found at harvest (Fig. 2, Table 4). Drought-stressed M+ C0 plants produced a shoot mass comparable to S- plants.

Grain yield

The effect of AM fungi was only significant in drought-stressed C0 plants (Fig. 3, Table 4). Drought stress decreased the final grain yield of C0 by 55% compared with S- plants, but the reduction was only 31% in the presence of AM colonization. After the drought treatment, AM C0 plants had a grain yield comparable to that of C8 plants with or without AM colonization. The mycorrhizal dependencies of grain yield in C0 and C8

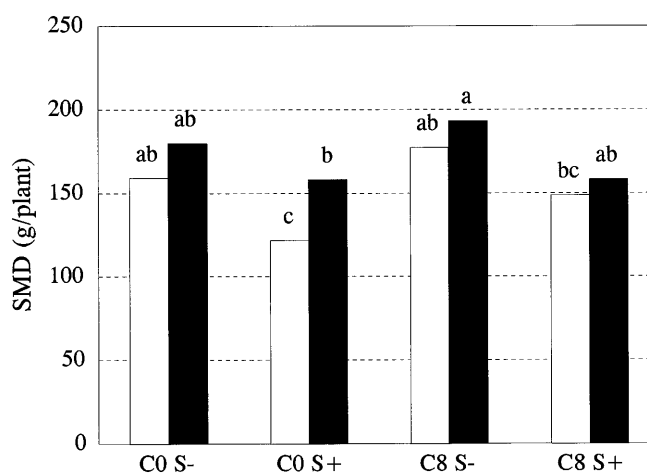


Fig. 1 Mean shoot mass after drought (SMD) of maize cultivars C0 and C8 under well-watered (S-) or drought-stressed (S+) conditions ($n=4$) with (filled columns) or without (open columns) arbuscular mycorrhizal (AM) colonization. Means with different letters are significantly different at $P \leq 0.05$

Table 3 Means ($n=3$) and standard errors (in parentheses) for nutrient content (mg/plant) in grains of drought-sensitive and -resistant maize cultivars at the harvest stage after drought-stressed or well-watered conditions with (M+) or without (M-)

arbuscular mycorrhizal colonization. Different letters within a column indicate significant differences ($P \leq 0.05$) using Tukey's Studentized Range (HSD) test

	N	P	K	Ca	Mg	S	Fe	Mn	Cu	Zn
<i>Drought-sensitive (C0) cultivar</i>										
Drought-stressed										
M+	1589 ^e (58)	263 ^{cd} (26.0)	464 ^b (47.2)	484 ^{cd} (102)	280 ^b (8.5)	92.1 ^{bc} (9.5)	8.62 ^{bc} (1.09)	4.10 ^{bc} (0.17)	0.57 ^{cd} (0.02)	44.1 ^c (5.7)
M-	688 ^f (48)	169 ^d (23)	331 ^b (2)	347 ^d (24.3)	159 ^c (21.1)	60.5 ^c (12.1)	5.20 ^c (0.79)	2.09 ^{ef} (0.22)	0.31 ^d (0.07)	47.7 ^c (0.4)
Well-watered										
M+	2108 ^{cd} (134)	472 ^a (36)	671 ^a (110)	1591 ^a (71.0)	433 ^a (49.9)	176 ^a (9.2)	19.8 ^a (0.30)	6.34 ^a (0.38)	0.70 ^a (0.18)	40.9 ^{cd} (4.3)
M-	1720 ^{de} (45.5)	427 ^{ab} (64)	739 ^a (37.9)	985 ^b (48.5)	489 ^a (18.6)	125 ^{ab} (11.5)	17.8 ^a (3.57)	5.01 ^{ab} (0.40)	0.51 ^{cd} (0.04)	102 ^a (2.3)
<i>Drought-resistant (C8) cultivar</i>										
Drought-stressed										
M+	2673 ^b (41)	427 ^{ab} (47)	894 ^a (27.7)	721 ^{bc} (78.5)	229 ^{bc} (10.4)	160 ^a (13.9)	8.19 ^{bc} (0.94)	1.76 ^f (0.13)	0.34 ^{cd} (0.01)	56.4 ^{bc} (4.6)
M-	1583 ^c (135)	244 ^{cd} (32)	475 ^b (23.3)	432 ^{cd} (38.9)	246 ^{bc} (15.5)	135 ^{ab} (14.8)	12.7 ^{ab} (0.72)	2.73 ^{cd} (0.19)	0.59 ^{cd} (0.03)	26.5 ^d (3.1)
Well-watered										
M+	3604 ^a (163)	391 ^{abc} (24.5)	836 ^a (13.9)	1659 ^a (229)	559 ^a (53.1)	190 ^a (24.4)	18.9 ^a (1.36)	3.69 ^c (0.14)	1.06 ^a (0.11)	75.7 ^b (4.70)
M-	2532 ^{bc} (43)	509 ^a (18)	905 ^a (54.0)	830 ^{bc} (92.4)	414 ^a (22.2)	189 ^a (13.4)	20.0 ^a (0.68)	1.63 ^f (0.08)	0.85 ^{ab} (0.09)	37.2 ^b (2.8)
ANOVA: C (cultivar), S (drought treatment), M (mycorrhizal treatment)										
C	***	*	***	NS	NS	***	*	***	**	*
S	***	***	***	***	***	***	***	***	***	***
M	***	*	***	***	*	*	NS	***	NS	NS
C X S	NS	*	**	NS	NS	NS	NS	***	*	NS
C X M	**	NS	NS	NS	NS	NS	*	**	*	***
S X M	*	**	**	**	NS	NS	NS	**	NS	***
C X S X M	NS	*	**	NS	***	NS	NS	***	*	***

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.001$ NS not significant

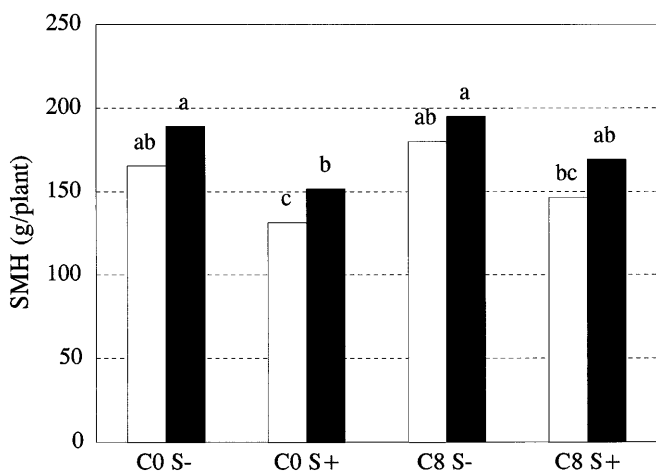


Fig. 2 Mean shoot mass at harvest (SMH) of maize cultivars C0 and C8 under well-watered (S-) or drought-stressed (S+) conditions ($n=4$) with (filled columns) or without (open columns) AM colonization. Means with different letters are significantly different at $P \leq 0.05$

were 14.7% and 8.01% under well-watered and 42.9% and 14.4% under drought-stressed conditions, respectively.

Harvest index

The drought treatment significantly decreased the HI for M- and M+ plants of both cultivars. (Fig. 4, Table 4), but HI values were significantly higher in M+ than M- plants of C0 under drought conditions. The HI values for drought-stressed AM plants of C0 were comparable to those for drought-stressed C8 plants, either with or without AM inoculation.

Reproductive behaviour

The days to tassel emergence (DTE), days to silk emergence (DSE), and ASI were significantly lower with the drought-resistant (C8) than with the drought-sensitive (C0) cultivars (Tables 4, 5). However, drought stress

Table 4 ANOVA for shoot mass after drought (SMD) and at harvest (SMH), grains (GRN), harvest index (HI), days to tassel emergence (DTE), silk emergence (DSE), and anthesis-silking interval (ASI)

	SMD	SMH	GRN	HI	DTE	DSE	ASI
Cultivars (C)	*	*	***	***	***	***	***
Stress (S)	***	***	***	***	NS	NS	NS
Mycorrhizae (M)	***	***	***	***	***	***	***
C X S	NS	NS	NS	***	NS	NS	NS
C X M	NS	NS	NS	*	*	NS	NS
S X M	NS	NS	NS	*	NS	NS	NS
C X S X M	NS	NS	NS	NS	NS	NS	NS

* $P \leq 0.05$ ** $P \leq 0.001$ NS not significant

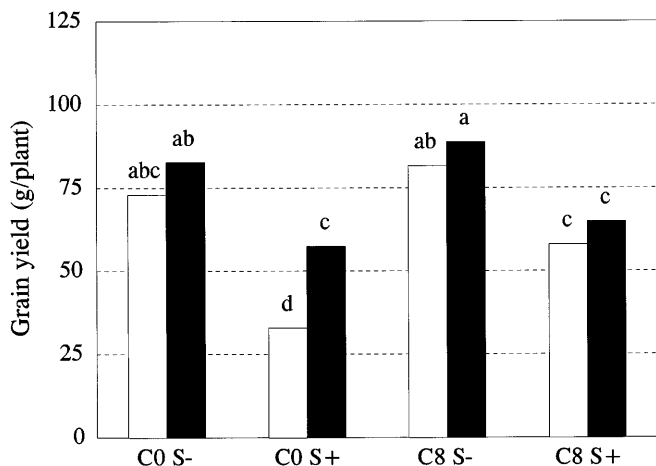


Fig. 3 Mean grain yields of maize cultivars C0 and C8 under well-watered (S^-) or drought-stressed (S^+) conditions ($n=4$) with (filled columns) or without (open columns) AM colonization. Means with different letters are significantly different at $P \leq 0.05$

had little impact on DTE (Table 5) as the plants were only exposed at the beginning of drought treatment. The lowest DTE value was obtained for the well-watered M+ plants of C8. AM inoculation significantly reduced the DSE of C0 under both conditions (Table 5). The DSE values of M+ plants of C0 were significantly lower than M- plants with or without drought treatment. As a result, ASI values (Table 5) of M+ C0 plants were significantly lower than those of M- plants. In comparison to C8 plants, ASI values for C0 were 3.2 and 3.8 times higher in M+ and M- plants, respectively.

Discussion

Inoculation of tropical maize cultivars having differential sensitivity to drought with the AM fungus *G. intraradices* had a beneficial effect on plant nutrition, growth, grain yield, and reproductive behaviour during and after moderate drought stress conditions. The results of this study suggest that AM inoculation im-

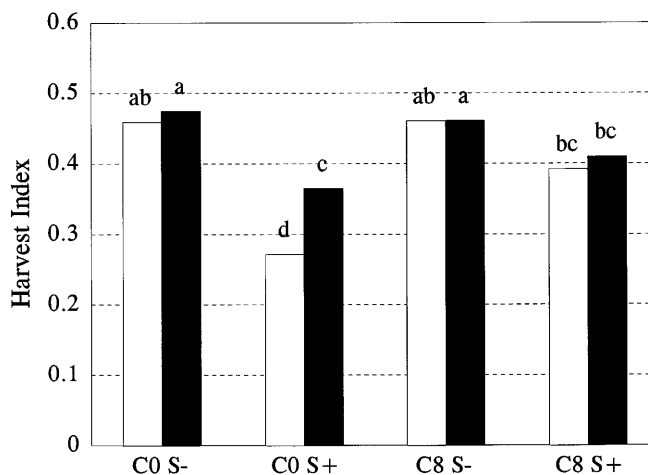


Fig. 4 Mean harvest index (HI) of maize cultivars C0 and C8 under well-watered (S^-) or drought-stressed (S^+) conditions ($n=4$) with (filled columns) or without (open columns) AM colonization. Means with different letters are significantly different at $P \leq 0.05$

Table 5 Means ($n=4$) and standard errors (in parentheses) of DTE, DSE, and ASI for drought-sensitive and -resistant maize cultivars after drought-stressed or well-watered conditions with (M+) or without (M-) arbuscular mycorrhizal colonization. Different letters within a column indicate significant differences ($P \leq 0.05$) using Tukey's Studentized Range (HSD) test

	DTE	DSE	ASI
<i>Drought-sensitive (C0) cultivar</i>			
Drought-stressed			
M+	73.8 ^a (1.0)	85.5 ^b (0.6)	11.8 ^b (1.3)
M-	74.0 ^a (0.8)	88.0 ^a (1.8)	14.0 ^a (2.3)
Well-watered			
M+	74.0 ^a (0.8)	84.8 ^b (1.7)	10.8 ^b (1.0)
M-	74.0 ^a (1.2)	87.5 ^a (0.6)	13.5 ^a (1.3)
<i>Drought-resistant (C8) cultivar</i>			
Drought-stressed			
M+	70.5 ^{ab} (0.6)	74.3 ^c (0.5)	3.80 ^c (0.5)
M-	72.3 ^{ab} (0.5)	76.0 ^c (0.0)	3.80 ^c (0.5)
Well-watered			
M+	70.0 ^c (0.8)	73.8 ^c (1.3)	3.80 ^c (0.5)
M-	71.5 ^{bc} (0.6)	72.3 ^c (1.5)	3.80 ^c (1.5)

proves drought tolerance of maize cultivars through the enhanced uptake of slowly diffusing mineral ions such as PO_4^- , Ca^{2+} , Cu^{2+} , and Zn^{2+} . Our results agree with the findings of Sylvia et al. (1993), who reported that AM inoculation with *G. fasciculatum* increased the concentrations of P and Cu in both shoots and grains of field-grown maize under increasing intensities of

drought stress. According to Kothari et al. (1990) in maize and Raju et al. (1990) in sorghum, the enhanced host plant nutrition resulting from AM colonization may be explained by a greater absorption surface area or proliferated root growth.

Numerous greenhouse and field experiments have demonstrated conclusively that plants colonized by AM fungi are much more efficient in taking up soil P than non-AM plants (Smith and Gianinazzi-Pearson 1988; McGonigle and Miller 1993; Augé et al. 1994; Asmah 1995). In our study, AM colonization increased grain P content under drought conditions. Our earlier study (Subramanian et al. 1995) indicated that AM maize plants maintained higher (less negative) leaf water potentials than non-AM plants even after 3 weeks of drought stress. The results here agree with the findings of Nelsen and Safir (1982), who observed that improved P nutrition enabled AM onion plants to maintain higher leaf water potentials despite a more negative soil water potential. Our results also indicate that, in addition to enhanced P nutrition, N content increases considerably in shoots and grains under drought conditions. Tobar et al. (1994a, b) showed a direct effect of AM fungus on N acquisition by lettuce plants grown in drought-stressed soil. Root colonization with AM fungi enhanced the uptake of N and P, which resulted in higher shoot mass production under drought conditions. The increased P status of AM plants may have allowed the host plant to absorb more Zn^{2+} and Cu^{2+} (Jarrell and Beverly 1981). Pai et al. (1994) indicated an increase in Ca uptake by AM-inoculated cowpea plants, which in turn helped the plants withstand drought by improving host plant water relations.

In the present study, the higher shoot mass of AM plants may be related to increased nutrient content of immobile elements such as P, Cu, and Zn. Medeiros et al. (1994) observed a significant positive correlation between biomass and nutrient content in sorghum. Subramanian et al. (1995) showed that AM maize plants under drought conditions had higher leaf water potentials and lower stomatal resistances indicating that the stomata of these plants remained open longer than those of non-AM plants. We previously indicated that AM plants under drought conditions retained more sugars than non-AM plants (Subramanian and Charest 1995), which is physiologically important for tolerance of drought and recovery after drought stress (Kameli and Lösel 1993). Consequently, AM-colonized maize plants retained a 27.5% higher green leaf area than non-AM plants, especially in the sensitive cultivar under drought conditions, and thus contributed to enhanced shoot mass (Subramanian et al. 1995).

In our study, the beneficial effect of AM inoculation was more pronounced in the drought-sensitive C0 cultivar, as indicated by grain yield and mycorrhizal dependency. The increased HI of AM plants thus suggests that significant amounts of nutrients, especially N, P, and assimilates, were translocated from the source to

the sink to support kernel development and grain yield. Schussler and Westgate (1994) observed that decreasing the amount of reserve assimilate at flowering increased the vulnerability of kernel set to lowered water potential in field-grown maize plants. Recently, Zinselmeier et al. (1995) showed that the assimilate supply in water-deficient maize plants is not sufficient to maintain newly formed zygotes, and that this leads to zygotic abortion and kernel set. With AM colonization, maize plants were able to supply nutrients and assimilates for kernel growth, thus mitigating reduction of grain yield under water-deficit conditions.

ASI is one of the most important parameters considered during the evaluation of drought-resistant strains for water-deficit environments (Fischer et al. 1989). The observed differences here in ASI values between C0 and C8 are consistent with the study of Bolaños and Edmeades (1993b), who reported that ASI is a heritable trait which decreases as selection progresses. These authors stressed that maize yield was reduced as much as 90% as the ASI increased from 0 to 10 days. In our study, shortening of the ASI by 2 days in the mycorrhizal, drought-sensitive C0 cultivar may have contributed to its higher grain yield.

In summary, AM colonization appears to improve host plant nutrition under drought conditions. The AM response was more pronounced in drought-sensitive than -resistant cultivars. Improved plant nutrition due to AM colonization promoted plant growth, which in turn shortened the ASI of the drought-sensitive C0 cultivar, and thus produced higher grain yield under drought conditions. This study reveals that AM inoculation enhances the nutritional status of tropical maize and enables these host plants to sustain moderate drought conditions.

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