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Comparative Responses to Arbuscular Mycorrhizal Fungi of Maize Cultivars Different in Downy Mildew Resistance and Fertilizer Requirement

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ABSTRACT: A pot experiment was carried out with a sterilized soil to compare the enhancement of growth due to arbuscular mycorrhizal (AM) fungal inoculation in maize cultivars that differ in downy mildew resistance (DMR) and in their fertilizer requirements to attain maximum yields. A 4 x 3 factorial in complete randomized block design with 3 replications was employed. The first factor comprised two open-pollinated maize cultivars and two maize hybrids. The former two were Suwan-1 selection cycle 0 (SW1C0), a non-DMR cultivar and Suwan-1 selection cycle 11 (SW1C11), a cultivar with high yield at high soil fertility and DMR. The latter two were Suwan 2301 (SW2301), a cultivar requiring low rates of N and P fertilizers, and Suwan 3851 (SW3851), a cultivar requiring high rates of N and P fertilizers, both of which were downy mildew resistant. The second factor comprised three AM fungal inoculation practices, namely, non-inoculated with AM fungi, inoculated with *Scutellospora fulgida* and inoculated with *Glomus aggregatum*. The DMR and non-DMR maize cultivars gave comparable responses to AM fungi. The cultivar requiring high rate of fertilizers was lower in its response to AM fungi in P and K uptake than the cultivar requiring low rate of fertilizers. The lower response in P uptake was explained by higher P utilization efficiency of the cultivar whereas the lower response in K uptake was not related to K utilization efficiency of the cultivar. The maize cultivars lower in nutrient (N, P and K) efficiencies or in shoot dry weight gave greater responses to AM fungi in shoot dry weight.

KEYWORDS: arbuscular mycorrhizal fungi, downy mildew resistance, fertilizer requirement, maize.

INTRODUCTION

Differences in responses of plants to arbuscular mycorrhizal (AM) fungi can be found not only among plant species but also among cultivars of the host plant[1]. Manske[2] found that improved, high yielding wheat (*Triticum aestivum*) cultivars were less responsive to AM fungus than landrace cultivars, whereas Zhu et al[3] found that an improved barley (*Hordeum vulgare* L.) cultivar was less responsive to AM fungi than a landrace barley. These results suggest that, in some cases, crop improvement reduces the response of crops to AM fungi. From experimental investigation with maize and wheat, Toth et al[4] and Hetrick et al[5] hypothesized that increasing resistance of crops to fungal pathogens by plant breeding decreases the benefit from AM fungal symbiosis.

In Thailand, the maize breeding program has been primarily aimed at improving maize for high yielding potential. However, some effort has also been made to breed drought-tolerant maize cultivars. The maize cultivars that have been most consistently improved for high yielding potential is Suwan-1 (SW1), an open-pollinated composite cultivar, and the most prominent drought-tolerant cultivar so far produced is Suwan 2301 (SW2301) hybrid. SW1 has now been improved for more than 11 selection cycles. Grain yield of SW1 after 11 selection cycles is 6.7 t/ha, as compared to 3.6 t/ha obtained from the non-improved SW1 grown under the same conditions[6]. It has been found that the improvement of SW1 maize also improved its resistance to downy mildew, a fungal disease. For example, Sriwatanapongse et al[7] reported that downy mildew infection of SW1 plants from selection cycle 7 was less than 5%, whereas that of the non-improved SW1 plant was 80%. In addition to being drought-tolerant, SW2301 has been found to required lower rates of fertilizers than other tested maize cultivars to attain maximum yield[8,9]. AM fungi are known to enhance drought tolerance[10] and lower the fertilizer requirement of the host plant[11,12]. For example, Suwan-2 maize inoculated with *G. aggregatum* and Suwan-2 non-

inoculated with AM fungi but supplied with 125 kg P_2O_5/ha were reported to give comparable shoot dry matter[12]. The improved drought-tolerance and the low fertilizer requirement found in SW2301 presumably were results of superior response to AM fungi of SW2301 plants. The work reported herein was carried out to compare responses to AM fungi of maize cultivars different in downy mildew resistance (DMR) and in fertilizer requirement.

Materials and Methods

Experimental Design

A pot experiment using a 4 x 3 factorial in randomized complete block design with 3 replications was carried out under a plastic roof at the Department of Soil Science, Kasetsart University, Bangkok, Thailand. The two factors were 4 maize cultivars and 3 AM fungal inoculation practices. The maize cultivars included two open-pollinated cultivars, namely Suwan-1 selection cycle 0 (SW1C0) and Suwan-1 selection cycle 11 (SW1C11) and two hybrids, namely Suwan 2301 (SW2301) and Suwan 3851 (SW3851). The AM fungal inoculation practices were : (1) non-inoculated with AM fungi, (2) inoculated with *Scutellospora fulgida* and (3) inoculated with *Glomus aggregatum*.

SW1C0 maize represented non-DMR cultivars whereas SW1C11 represented DMR cultivars. SW2301 and SW3851, which were DMR hybrids, were used as cultivars requiring low and high fertilizer (N and P) rates to attain their maximum yields, respectively. SW2301 was reported to require 90-90 kg N-P_2O_5/ha to reach a maximum grain yield of 4.25 t/ha, whereas the other four tested cultivars required 120-120 kg N-P_2O_5/ha or more to reach their maximum yields of 5.7 t/ha or more[8]. SW3851 was reported to require more than 180-180 kg N-P_2O_5/ha to attain its maximum yield of 6.58 t/ha, whereas the other three cultivars required 60-60 to 120-120 kg N-P_2O_5/ha to attain their maximum yields of 4.31 t/ha or more[13].

AM Fungal Preparation

The AM fungal species were collected from the field in Thailand by Boonlue[14] and had been maintained with pot culture on Pak Chong soils. Spores were collected by the wet-sieving and decanting method[15]. Single spore cultures were done with maize grown on fired clay (Terragreen®) at CPB-CNRS, Nancy, France. The soil inoculum production was performed with maize grown on Pak Chong soils at Kasetsart University. Morphotype of spores were observed to detect contamination in the pot cultures. The soil inoculum of each AM fungal species included the infected roots, hyphae and spores (about 1 spore/g soil) without contamination of any other AM fungal species.

Soil and Pot Preparation

The soil used was Pak Chong series (Rhodic Kandiustox, very fine, kaolinitic, isohyperthermic) collected from the National Corn and Sorghum Research Center, Nakhon Ratchasima province. The soil (with 13 ppm P by Bray-II method) was sterilized with Dazomet (Basamid®, 60 g/100 kg soil) according to Suwanarit et al[16]. Plastic pots and saucers were sterilized by spraying with 70% ethanol. Then, 7 kg of the sterilized soil was weighed out into each plastic pot.

Planting, Inoculation and Growth

Eight seeds was buried 1 cm below the surface of 300 g soil inoculum contained in a pitch in each pot[16]. The inoculum was then covered with 1-cm layers of sterilized soil and expanded clay (Hydroton®), respectively. Three hundred grams of sterilized soil was applied instead of soil inoculum in the pots for the non-inoculated AM fungal treatment. The seedlings were thinned to 3 plants per pot at 10 days after planting (DAP). The temperature during the experiment in the plastic house fluctuated between 18 and 45°C. The plants were liberally supplied with distilled water throughout the growing period by spraying water on the soil surface. No chemical was applied to the plants. The positions of pots in each replication were rerandomized weekly until tasseling. After silking of 50% of the plants in all treatments, watering was stopped. The plants were cut just above the soil surface at 90 DAP and the shoots were ovened at 70°C until constant weight before weighing.

Data Collection and Calculation

The height of plants were measured at 30, 45, and 62 DAP. The tasseling and silking ages and dry weight of plant shoots at 90 DAP were recorded. Ground samples of shoot were digested with H_2SO_4 + Na_2SO_4 + Se (100: 10: 1) digestion mixture. N, P and K in the digest were measured with micro Kjeldhal distillation[17], the vanadomolybdophosphoric yellow colorimetric method using a Spectronic-21 colorimeter[18], and a frame emission spectrophotometer, respectively. After cutting the plant shoot, the soil was allowed to dry out within two weeks. All of the soil of each pot was then taken out of the pot, mixed well and malleted to pass a 2-mm sieve. One hundred grams of soil was used for examining the number of spores of the inoculated AM fungal species/100 g soil using the wet sieving and decanting method[15]. The enhancing effects of AM fungal inoculation on maize plants were presented as percentage increase or decrease, calculated as:

$$\text{Increase or decrease (\%)} = \left[\frac{(\text{Mi} - \text{Mni})}{\text{Mni}}\right] \times 100$$

where M_i and M_{ni} were the values of the parameters of maize plants with and without AM fungal inoculation, respectively.

Statistical Analysis

Analysis of variance was used to determine the effects of AM fungal inoculation x maize cultivar interactions on maize growth using the IRRISTAT program of the International Rice Research Institute. Duncan's Multiple Range Test ($DMRT_{0.05}$) was used for comparison of the effects between various AM fungal inoculations within a maize cultivar. The shoot dry weight, N, P and K efficiencies of non-inoculated plants and spore intensity in soil were compared using standard errors.

Results

Plant Height

At 30 and 45 DAP, the plants inoculated with AM fungi were taller than non-inoculated plants (Fig 1a and 2a). However, the heights of plants inoculated with *G. aggregatum* was comparable to those of plants inoculated with *S. fulgida*, except the height at 30 DAP, in which SW3851 plants inoculated with *G. aggregatum* were taller than plants inoculated with *S. fulgida*. Percentage increases in height in response to the two AM fungi were comparable in all maize cultivars (Fig 1b and 2b).

At 62 DAP, there was no significant difference in height between inoculation and non-inoculation in maize cultivars SW2301 and SW3851. However, the AM inoculated plants were taller than the non-inoculated plants in the case of SW1C11. The SW1C0 plants inoculated with *S. fulgida* were taller than non-inoculated plants, and tended to be taller than the plants inoculated with *G. aggregatum* (Fig 3a). Percentage increases in height in response to the two AM fungi were comparable in all maize cultivars (Fig 3b).

Tasseling and Silking Ages

The tasseling and silking ages of the AM fungal inoculated plants were shorter than those of the non-inoculated plants (Fig. 4a and 5a, respectively). The results of the present study were similar to the previous findings of Subramanian and Charest[19] that the emergence of tassels and silks were earlier in AM fungal inoculated plants than in non-inoculated plants.

Percentage decreases in the flowering ages in response to the two AM fungi were comparable in all maize cultivars (Fig 4b and 5b).

Shoot Dry Weight

The plants inoculated with AM fungal species gave greater shoot dry weight than non-inoculated plants (Fig 6a). Percentage increases in shoot dry weight in response to the two AM fungi were comparable in all maize cultivars (Fig 6b).

N Uptake

The inoculation of SW2301 with *S. fulgida* or *G. aggregatum* gave greater N uptake in shoots than non-inoculation. The inoculation of SW1C11 with *S. fulgida* gave greater N uptake than non-inoculation, whereas its inoculation with *G. aggregatum* also tended to increase N uptake. The inoculation of SW1C0 and SW3851 cultivars with AM fungi did not show significant enhancing effects (Fig 7a). Percentage increases in N uptake in response to the two AM fungi were comparable in all maize cultivars (Fig 7b).

P Uptake

Inoculation with *S. fulgida* gave a significant enhancing effect on P uptake in the case of SW2301, but showed no significant effect in the cases of SW1C0, SW1C11 and SW3851. Inoculation with *G. aggregatum* showed significant enhancing effects in the cases of SW2301 and SW3851 but showed no significant effect in the cases of SW1C0 and SW1C11 (Fig 8a). Percentage increases in P uptake in response to AM fungi were

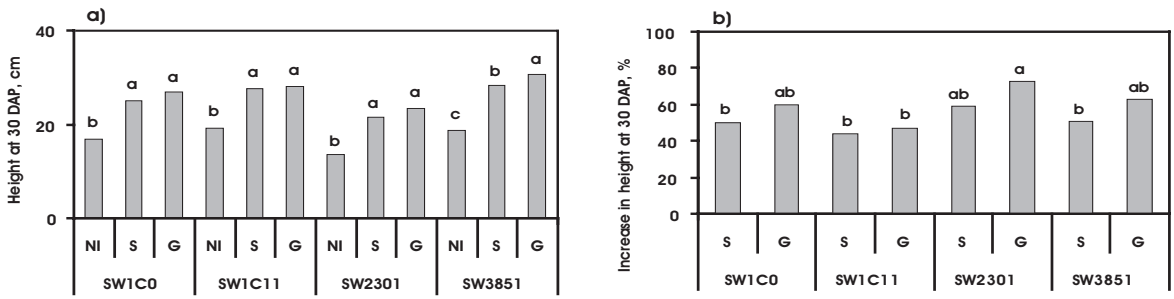

Fig 1. Height (a) and increase in height compared with that of NI (b) of maize at 30 DAP, as affected by maize cultivar and AM fungal species. Means with a common letter are not significantly different at $P \leq 0.05$ within the same maize cultivars in (a) and within all samples in (b). NI = non-inoculated with AM fungi; S = inoculated with *Scutellospora fulgida*; G = inoculated with *Glomus aggregatum*.

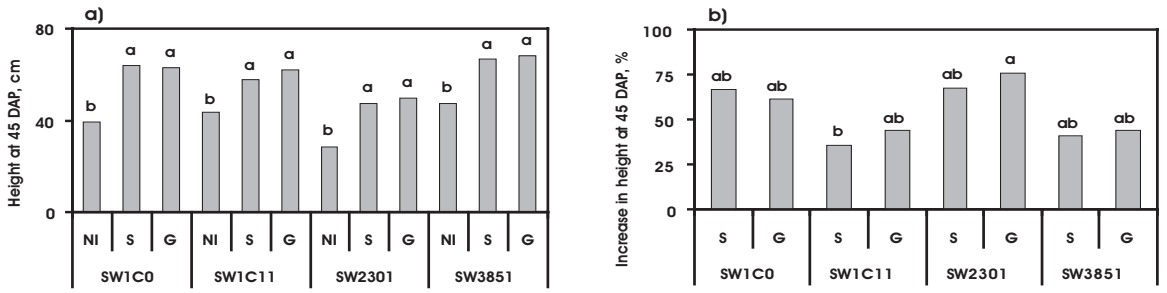

Fig 2. Height (a) and increase in height compared with that of NI (b) of maize at 45 DAP, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

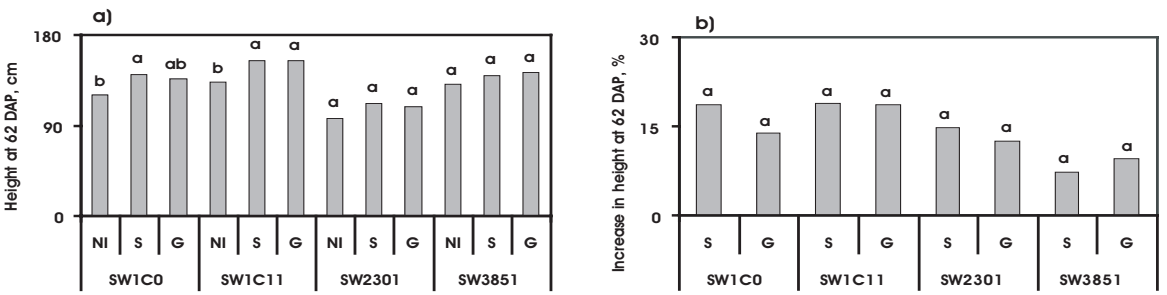

Fig 3. Height (a) and increase in height compared with that of NI (b) of maize at 62 DAP, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

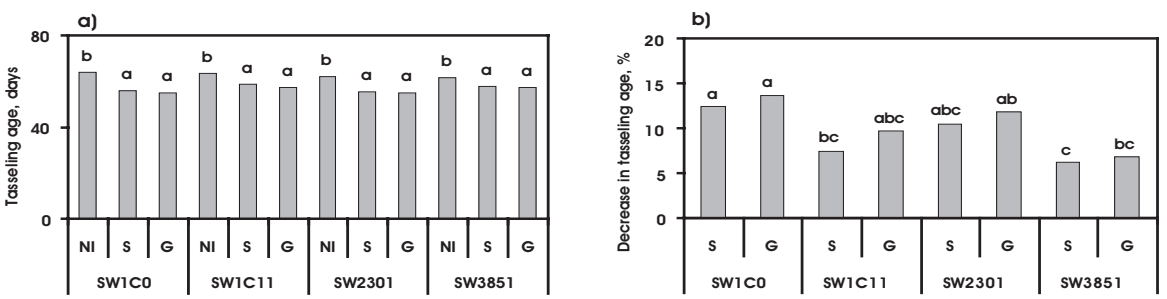

Fig 4. Tasseling age (a) and decrease in tasseling age compared with that of NI (b) of maize, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

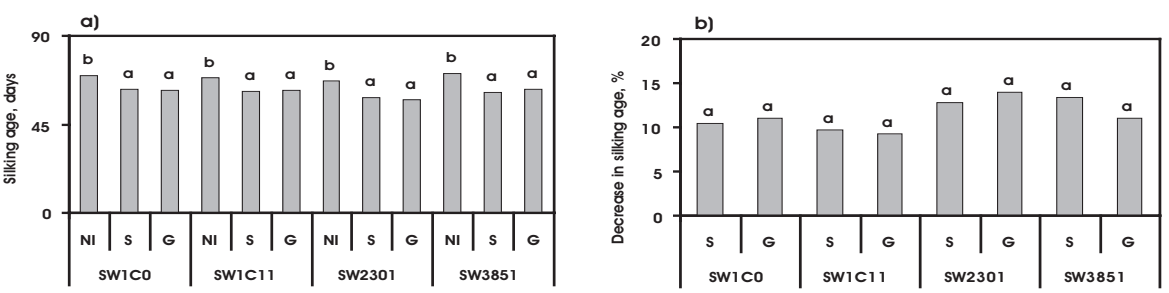

Fig 5. Silking age (a) and decrease in silking age compared with that of NI (b) of maize, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

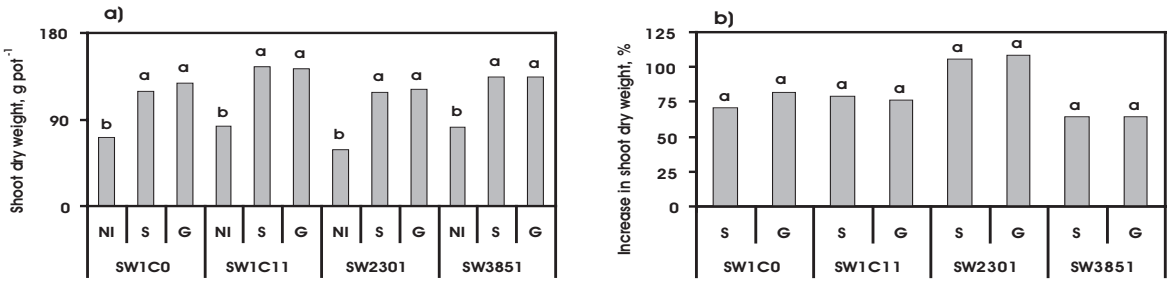

Fig 6. Shoot dry weight (a) and increase in shoot dry weight compared with that of NI (b) of maize, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

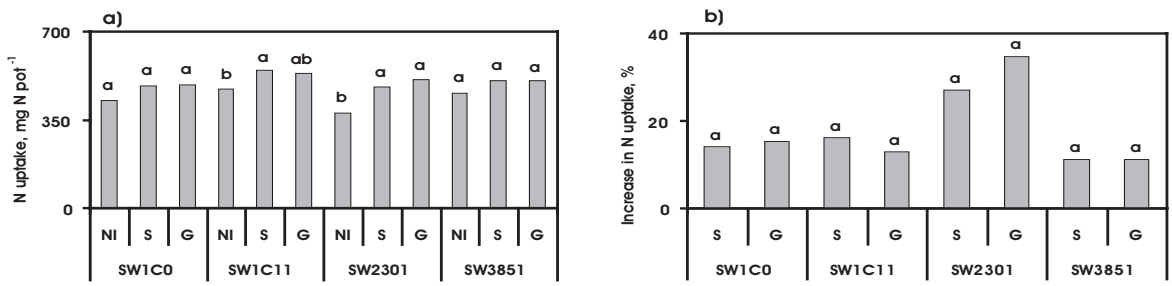

Fig 7. N uptake in shoot (a) and increase in N uptake in shoot compared with that of NI (b) of maize, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

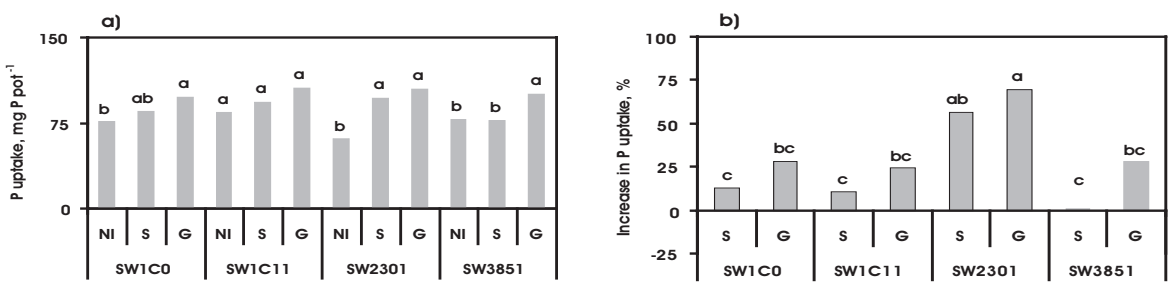

Fig 8. P uptake in shoot (a) and increase in P uptake in shoot compared with that of NI (b) of maize, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

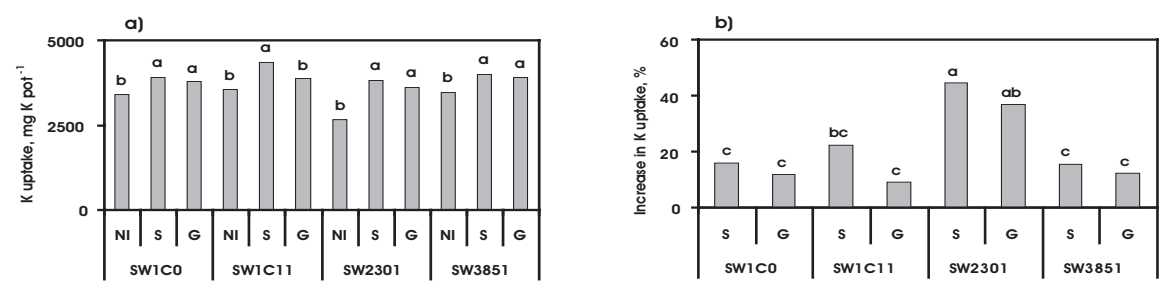

Fig 9. K uptake in shoot (a) and increase in K uptake in shoot compared with that of NI (b) of maize, as affected by maize cultivar and AM fungal species. Refer to Fig 1 for the meanings of the captions.

comparable between the two AM fungi and between SW1C0 and SW1C11 (Fig 8b). However, percentage increases in P uptake in response to each of the two AM fungi in the case of SW2301 were higher than those in the case of SW3851. With the same maize cultivar, the two AM fungi showed comparable percentage increases.

K Uptake

Inoculation with either of the two AM fungi gave greater K uptake than non-inoculation, with the exception that the SW1C11 plants inoculated with *G. aggregatum* did not significantly affect K uptake (Fig 9a). The percentage increases in K uptake in response to AM fungi were comparable between the two AM fungi and between SW1C0 and SW1C11 (Fig 9b). However, the responses of SW2301 to each of the two AM fungi were higher than those of SW3851. With the same maize cultivar, the two AM fungi showed comparable responses.

AM Fungal Spore Intensity in Soils

There was no difference between intensity of spores of each AM fungal species in the inoculation treatments, whereas the studied AM fungal species were not found in the non-inoculation treatment (Fig 10). This showed that the inoculation was effective. Furthermore, no contamination of AM fungal species between treatments of AM fungal inoculation was detected.

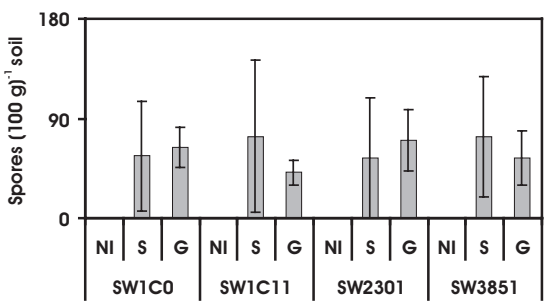

Fig 10. Spore intensity of the inoculated AM fungal species in soil after harvest. The range on the top of each bar is the standard error. Refer to Fig 1 for the meanings of the captions.

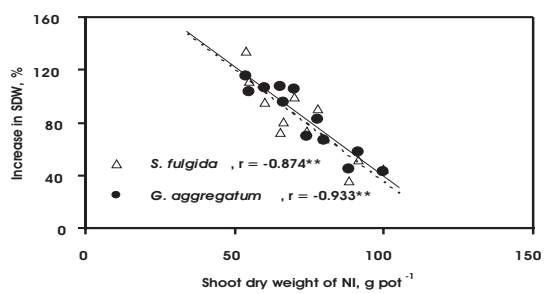

Fig 11. Relationship between shoot dry weight (SDW) of AM fungus non-inoculated plants (NI) and their responses in SDW to the two AM fungal species, *S. fulgida* (---) and *G. aggregatum* (—). ** Significant at $P \leq 0.01$.

Discussion

Mycorrhizal Response of Non-DMR and DMR Maize

SW1C0 and SW1C11 gave comparable responses to *G. aggregatum* and *S. fulgida* in all plant parameters (Fig 1b, 2b, 3b, 5b, 6b, 7b, 8b and 9b), with the exception of the tasseling age in which SW1C0 gave a higher response to *S. fulgida* than SW1C11 (Fig 4b). This suggests that the non-DMR and DMR maize cultivars are comparable in their responses to AM fungi. The lower response to AM fungi in tasseling age did not seem to be a result of DMR because SW2301, a DMR hybrid, showed a response similar to SW1C0 when inoculated with *S. fulgida*.

Comparison between the non-DMR (SW1C0) and DMR (SW1C11) cultivars in plant height at different ages, flowering ages, shoot dry weight and nutrient uptake indicated that there was no significant effect of improvement of maize cultivar yield at high soil fertility and DMR on response to AM fungi. Furthermore, SW2301, which is a DMR hybrid, gave greater responses to AM fungi in P and K uptake than the non-DMR cultivar (Fig 8b and 9b). This finding does not support the hypothesis of Toth et al[4] and Hetrick et al[5] that increasing resistance of crops to fungal pathogens and yield at high soil fertility decreases the benefit from AM fungal symbiosis. The present results showed that resistance to downy mildew did not affect the benefit from mycorrhiza in maize.

Mycorrhizal Responses of Maize Cultivars Different in Fertilizer Requirement

SW2301 showed greater positive responses to *S. fulgida* and *G. aggregatum* in P and K uptake than SW3851

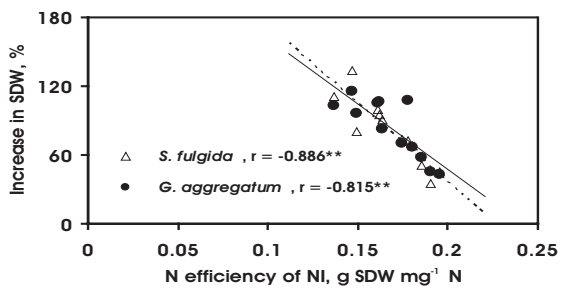

Fig 12. Relationship between N efficiency of AM fungus non-inoculated plants (NI) and their responses in SDW to the two AM fungal species, *S. fulgida* (---) and *G. aggregatum* (—). ** Significant at $P \leq 0.01$.

Table 1. Shoot dry weight (SDW) and N, P and K efficiencies of the maize cultivars obtained without AM fungal inoculation. Values are the means of three replicates with standard errors of the means.

Cultivars	SDW (g pot^{-1})	Nutrient efficiencies (g SDW mg^{-1} nutrient)		
		N	P	K
SW1C0	71.7±14.7	0.167±0.021	0.933±0.089	0.0210±0.0026
SW1C11	82.7±15.6	0.173±0.019	0.985±0.231	0.0233±0.0043
SW2301	58.1±6.4	0.154±0.022	0.940±0.058	0.0219±0.0018
SW3851	81.9±8.7	0.180±0.005	1.055±0.025	0.0236±0.0020

(Fig 8b and 9b), though these two maize cultivars gave comparable responses to the AM fungi in other plant parameters (Fig 1b, 2b, 3b, 4b, 5b, 6b and 7b). This supports the work of Linderman and Davis[20], who reported effects of different combinations between plant cultivars and AM fungal species on the advantages from AM fungal inoculation. They found that different AM fungi affected various cultivars of *Tagetes* spp. differently, in terms of the degree of plant growth enhancement.

The shoot dry weight and P utilization efficiency of maize plants without AM fungal inoculation (Table 1) may be used for prediction of the response to AM fungi in shoot dry weight of each maize cultivar[11,21]. The responses to AM fungi in shoot dry weight observed in the present study were highly negatively correlated to shoot dry weight of non-inoculated plants (Fig 11). The lower shoot dry weight of SW2301 compared to SW3851 might explain the greater response to AM fungi of this cultivar. This suggests that the lower shoot dry weight of the maize plant (Table 1) might be a cause of the higher response to AM fungi. This finding is supported by the results of Baon et al[21] and Kaeppler et al[11].

In addition, the responses to AM fungi in shoot dry weight were highly negatively correlated to N utilization efficiency of non-inoculated plants (Fig 12). The trend of lower N utilization efficiency in shoots of the hybrid requiring low rates of fertilizers (Table 1) might be a cause of the higher response to AM fungi. Tanaka and Yano[22] reported that *G. aggregatum* enhanced N uptake of maize. In the present study, the response of maize to *G. aggregatum* in N uptake was highly positively correlated with spore intensity of the fungus (Fig 13). Since Pitakdantham et al[12] found that the spore intensity of the fungus correlated with colonization in maize roots, these results suggested that N uptake of maize plant inoculated with *G. aggregatum* increased with increasing colonization in the roots. However, there was no correlation between the response in N uptake of maize plants inoculated with *S. fulgida* and spore intensity (Fig 13). This latter finding supported the results of Kaeppler et al[11] which showed that colonization was not correlated with response to AM fungi. The present results and the finding of Kaeppler et al[11] suggest that the enhancing effect on N uptake depend upon the AM fungal species.

The responses to AM fungi in shoot dry weight were highly negatively correlated to P utilization efficiency of non-inoculated plants (Fig 14). The higher P utilization efficiency in the shoots of hybrid maize plants requiring high rates of fertilizers (Table 1) might be a cause of the lower response to AM fungi. The present result supports those of Yao et al[23], Zhu et al[24] and Baon et al[21], who also found that the host plants with high P utilization efficiency gave lower mycorrhizal responses than those with lower P efficiency.

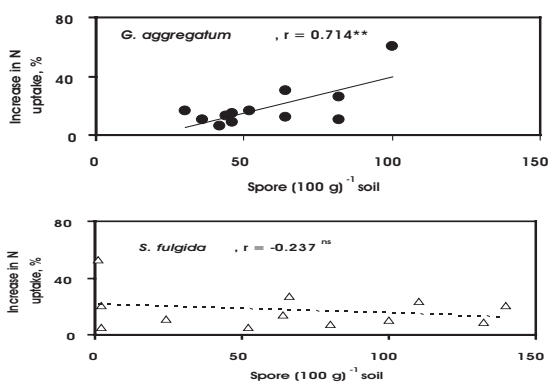

Fig 13. Relationship between spore intensity and responses in N uptake of the two AM fungal species. *S. fulgida* (---) and *G. aggregatum* (—). ** Significant at $P \leq 0.01$. ns not significant at $P \leq 0.05$.

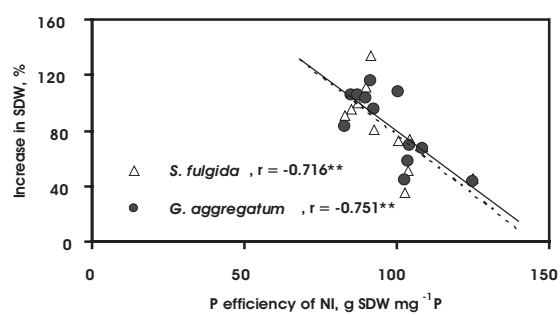

Fig 14. Relationship between P utilization efficiency of AM fungus non-inoculated plants (NI) and their responses in SDW to the two AM fungal species. *S. fulgida* (---) and *G. aggregatum* (—). ** Significant at $P \leq 0.01$.

Responses to *G. aggregatum* in shoot dry weight observed in the present experiment showed a negative correlation to the K utilization efficiency of the non-inoculated plants. However, the K utilization efficiency of the non-inoculated plants was not correlated with the response to *S. fulgida* (Fig 15). Accordingly, the K utilization efficiency of the non-inoculated plants (Table 1) might be used for prediction of the response in shoot dry weight to *G. aggregatum*, but not to *S. fulgida*. However, the two cultivars different in fertilizer requirement were not different in K utilization efficiency.

Therefore, lower shoot dry weight and lower nutrient (such as N and P) utilization efficiency of maize cultivars resulted in greater responses to AM fungi. The higher response to AM fungi in nutrient uptake might be a cause of the low fertilizer requirement to attain maximum yield and drought tolerance of SW2301. Sylvia et al[25] found that the proportional response of maize grain and biomass yield to inoculation with AM fungi increased with increasing drought stress. Improved nutrient status of AM plants may enable the host to absorb water more efficiently under drought conditions. The findings of Nelson and Safir[26], Osonubi[27] and Subramanian et al[28] that AM fungi enhanced drought tolerance and P uptake of their host plants suggests that a maize cultivar that requires lower soil fertility or a lower rate of P fertilizer, such as SW2301, would give a greater response to AM fungi than cultivars requiring high rates of P fertilizer. SW2301 is a well-known drought tolerant cultivar and has been used as a source of drought tolerance in breeding program[7].

The ability to acquire nutrients in the absence of AM fungi affected the degree of response to AM fungi. However, breeding to increase the benefit from mycorrhiza in increased fertilizer efficiency and selection of AM fungal species with persistent enhancing effects should be studied in order to reduce the cost of fertilization.

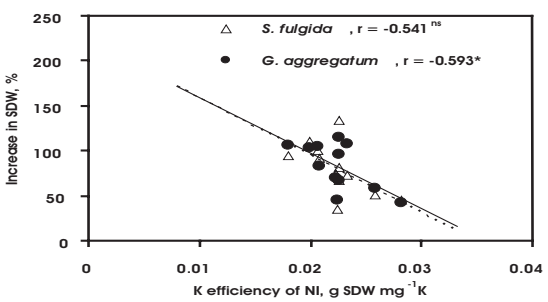

Fig 15. Relationship between K efficiency of AM fungus non-inoculated plants (NI) and their responses in SDW to the two AM fungal species. *S. fulgida* (---) and *G. aggregatum* (—). * Significant at $P \leq 0.05$. ns not significant at $P \leq 0.05$.

Conclusion

The DMR and non-DMR maize cultivars gave comparable responses to AM fungi. The cultivar requiring high rates of fertilizers was lower in its response to AM fungi in P and K uptake than was the cultivar requiring low rates of fertilizers. The lower response in P uptake was explained by the higher P utilization efficiency of the cultivar, whereas the lower response in K uptake was not related to K utilization efficiency of the cultivar. The maize cultivars lower in nutrient (N, P and K) utilization efficiencies or in shoot dry weight gave greater responses to AM fungi in shoot dry weight.

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