

Early mycorrhization of two tropical crops, papaya (*Carica papaya* L.) and pineapple [*Ananas comosus* (L.) Merr.], reduces the necessity of P fertilization during the nursery stage

Ana Sue RODRÍGUEZ-ROMERO^{1*}, Rosario AZCÓN², María Del Carmen JAIZME-VEGA¹

¹ Dep. Prot. Veg., Inst. Canar. Investig. Agrar., Apdo. 60, 38200 La Laguna, Tenerife, Spain
arguezr@icia.es

² Dep. Microbiol., Estac. Exp. Zaidín, CSIC, Prof. Albareda, 1, 18080 Granada, Spain

Early mycorrhization of two tropical crops, papaya (*Carica papaya* L.) and pineapple [*Ananas comosus* (L.) Merr.], reduces the necessity of P fertilization during the nursery stage.

Abstract — Introduction. The use of mycorrhizal fungi as biofertilizers can reduce chemical inputs during the nursery phase, allowing the production of high quality plant material with reduced fertilizer inputs. The lack of complete knowledge of each crop's responsiveness to mycorrhizal symbiosis, however, is still a handicap to the routine application of this biotechnology for commercial purposes. In our work, the influence of early mycorrhization as an alternative to standard P fertilization programs for two tropical crops, papaya and pineapple, was assessed in a greenhouse experiment. **Materials and methods.** Papaya seedlings and pineapple planting material were inoculated with the arbuscular mycorrhizal fungus (AMF) *Glomus mosseae* and cultured on substrates with increasing amounts of soluble P. Data concerning plant development and nutritional status were determined 5 months (papaya) and 7 months (pineapple) after inoculation. **Results.** For both crops, benefits derived from mycorrhization, expressed in terms of plant development and nutritional status, were significantly higher than those derived from P application. Overall, mycorrhizal papaya plants exhibited significantly higher biomass and macroelement contents in shoots than plants without mycorrhizas at any P level. Mycorrhizal effects on pineapple at the lowest P level were significant in terms of plant development and P shoot contents. **Conclusions.** Differential benefits derived from mycorrhization seem to be correlated to each crop's internal P requirements. Our work highlights the potential benefits of integrating early mycorrhization at the nursery stage in order to reduce P fertilizer inputs in sustainable plant production systems.

Spain / *Carica papaya* / *Ananas comosus* / juvenility of plants / fertilizer application / phosphate fertilizers / biofertilizers

La mycorrhization précoce de deux cultures tropicales, papayer (*Carica papaya* L.) et ananas [*Ananas comosus* (L.) Merr.], diminue la fertilisation en phosphore au stade pépinière.

Résumé — Introduction. L'utilisation de champignons mycorrhiziens comme biofertilisants peut réduire les intrants chimiques en pépinière, ce qui permet de produire des plants de haute qualité avec moindre apport d'engrais. Le manque de connaissances approfondies sur la réactivité de chaque culture à la symbiose mycorrhizienne est cependant encore un handicap pour l'application systématique de cette biotechnologie à des fins commerciales. Dans nos travaux, l'influence de la mycorrhization précoce utilisée en remplacement de programmes usuels de fertilisation en phosphore a été évaluée pour deux cultures tropicales, le papayer et l'ananas, dans une expérimentation en serre. **Matériel et méthodes.** Des plants de papayers et des rejets d'ananas ont été inoculés avec le champignon mycorrhizien à arbuscules (AMF) *Glomus mosseae* et cultivés sur substrats enrichis de quantités croissantes de P soluble. Des données sur le développement de la plante et son état nutritionnel ont été déterminées 5 mois (papayer) et 7 mois (ananas) après l'inoculation. **Résultats.** Pour les deux cultures étudiées, les bénéfices tirés de la mycorrhization, exprimés en termes de développement de la plante et de son état nutritionnel, ont été significativement plus élevés que ceux découlant de l'application de P. Dans l'ensemble, quelle que soit la quantité de P ajoutée au substrat, les papayers mycorrhizés ont présenté significativement des teneurs plus élevées en biomasse et en macroélément dans les tiges que les plantes sans mycorrhizes. L'effet des mycorrhizes sur l'ananas au plus bas niveau de P a été important vis-à-vis du développement de la plante et de la teneur en P de la tige. **Conclusions.** Les avantages différenciés provenant de la mycorrhization semblent être corrélés aux exigences spécifiques en P de chaque culture. Notre travail met en évidence les avantages potentiels de la mycorrhization précoce au stade de pépinière pour réduire les intrants en engrais phosphorés dans des systèmes durables de production végétale.

Espagne / *Carica papaya* / *Ananas comosus* / stade juvenile des plantes / fertilisation / engrais phosphate / biofertilisant

* Correspondence and reprints

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1. Introduction

Arbuscular mycorrhizal fungi (AMF) are obligate symbionts that colonize the roots of most cultivated plant species and can be found in nearly all types of ecological situations. They favor plant development by increasing plant tolerance to stress conditions such as salinity, drought, heavy metals and root soilborne pathogens, and the improvement of soil structure [1]. Nutrient uptake rates favored by mycorrhization have been frequently described for phosphorus (P), but also for nitrogen (N) acquisition [2, 3].

The use of arbuscular mycorrhizal fungi as biofertilizers in crop systems has increased in recent years. In the last decade, an increasing number of works suggest the inclusion of this biotechnology whenever possible, as a routine process for plant nursery production [4–6]. Early mycorrhization might reduce fertilizer and pesticide inputs during the nursery phase, while allowing the production of high quality plant material within a sustainable production process. One of the main handicaps of this proposal, however, is the lack of a complete knowledge of each crop's responsiveness and the effectiveness of mycorrhizal symbiosis, which are emergent properties of the interaction between plant and fungus species [7].

Most of the major crops in the tropics form beneficial associations with arbuscular mycorrhizal fungi [8]. Among them, papaya and pineapple, which are considered two of the most economically important [9], have been inoculated with mycorrhizal fungi with substantially different results [10–13].

The aim of our work was to compare the effects of the AMF *Glomus mosseae* and different P fertilization levels on the development and nutritional status of papaya and pineapple plants, in order to consider these symbionts as an alternative to P chemical fertilizers, during the nursery stage of plant production.

2. Materials and methods

2.1. Plant material

Papaya seedlings (*Carica papaya* L.) from cv. Sunrise seeds were grown in sterile sub-

strate consisting of a mixture of soil and vermiculite (1:1, v:v), with a low phosphorus content ($12.7 \text{ mg} \cdot \text{kg}^{-1}$ Olsen). Pineapple planting material [*Ananas comosus* (L.) Merr.] was “intermediate shoots” without roots of 60 g mean weight, taken from a traditionally-cultured adult plantation of cv. Smooth Cayenne. To develop roots in uncontaminated conditions, all pineapple material was first planted in the same sterile substrate used for papaya germination.

2.2. Fungus material

Glomus mosseae (Nicol. and Gerd.) Gerd. and Trappe, a collection isolate cultured under alfalfa [*Medicago sativa* (L.)] with a percentage of 62% of root colonization, was used. AMF inoculum (5 g per plant), consisting of rhizosphere soil containing pieces of mycorrhizal roots, hyphae and spores, was placed immediately below the seeds or plant material. Both papaya and pineapple were inoculated at the germination and rooting phase, respectively.

2.3. Phosphate treatments

Once mycorrhizas were established (ten weeks after AMF inoculation), plants were transplanted into individual pots filled with a sterile substrate mixture of soil and quartz silicon sand (1:1, v:v). The substrate chemical characteristics were: pH 6.5; E.C. $0.7 \text{ ds} \cdot \text{m}^{-1}$; $18.3 \text{ mg P Olsen} \cdot \text{kg}^{-1}$; $14.5 \text{ mg Fe} \cdot \text{kg}^{-1}$; $0.3 \text{ mg Mn} \cdot \text{kg}^{-1}$; $0.2 \text{ mg Zn} \cdot \text{kg}^{-1}$; $0.2 \text{ mg Cu} \cdot \text{kg}^{-1}$; $2.1 \text{ mg organic matter} \cdot \text{kg}^{-1}$; 40% base saturation; $3.7 \text{ mEq Ca} \cdot \text{L}^{-1}$; $2.3 \text{ mEq Mg} \cdot \text{L}^{-1}$; $1.5 \text{ mEq Na} \cdot \text{L}^{-1}$; $0.2 \text{ mEq K} \cdot \text{L}^{-1}$; $1.4 \text{ mEq Cl} \cdot \text{L}^{-1}$. The substrate was sterilized by autoclaving for 1 h at a time at $100 \text{ }^\circ\text{C}$ on each of three consecutive days.

The experimental soil was divided into four batches: P_0 was untreated control, of which a double quantity was prepared; P_1 , P_2 and P_3 were treatments receiving different doses of KH_2PO_4 . Dry potassium phosphate was mixed with the substrate. Substrates were kept at $19\text{--}25 \text{ }^\circ\text{C}$, with suitable watering for 2 weeks. Then, the plant-available P (Olsen) of each batch of soil was evaluated, resulting in: $P_0 = 18.3 \text{ mg} \cdot \text{kg}^{-1}$, $P_1 = 48 \text{ mg} \cdot \text{kg}^{-1}$, $P_2 = 79.4 \text{ mg} \cdot \text{kg}^{-1}$ and $P_3 = 100 \text{ mg} \cdot \text{kg}^{-1}$.

2.4. Experimental conditions and design

All plants were transferred to 3-L pots filled with the designated phosphate treatment substrate. Once they were transplanted, the experiment lasted for 3 months in the case of papaya plants, and 5 months in the case of pineapple plants. During the trial, plants were kept under greenhouse conditions ($T = 25\text{--}30\text{ }^{\circ}\text{C}$ and $\text{RH} = 70\text{--}90\%$), receiving 50 mL per pot of phosphorus-free nutrient solution [14] every 2 weeks. All pots were watered overhead daily.

An experiment with 5 treatments for each crop and 14 replicates per treatment was established: papaya [1 AMF P_0 + 4 control ($P_0\text{--}P_3$)] and pineapple [1 AMF P_0 + 4 control ($P_0\text{--}P_3$)]. One plant per pot was used as an experimental unit. Similar quantities of autoclaved inoculum and a soil extract solution (1:10 dilution) were added to the plants without mycorrhizas to minimize differences due to fungus inoculum application.

2.5. Assessment of variables

Shoot and root fresh weight (g) and shoot dry weight (g) were assessed as growing parameters at the end of the experiment for all plants.

Macroelements, *i.e.*, nitrogen, phosphorus and potassium, were determined on shoots ($\text{mg}\cdot\text{plant}^{-1}$). Samples were thoroughly washed in mild detergent, rinsed three times in distilled water, avoiding senescent or necrotic tissue, and prepared for foliar analysis. Samples were then dehydrated in a temperature-controlled fan-ventilated oven at $60\text{ }^{\circ}\text{C}$ for 24 h, ground in a ball mill and digested in wet acid [15], using nitric and perchloric acid. Analysis for all elements except nitrogen was done with a F586-587 Varian Liberty 220 inductively coupled plasma (ICP) emission spectrometer. Two readings were made per sample. Nitrogen content was determined according to the Kjeldahl procedure [16].

To assess mycorrhizal infection, a small root sample (5% of the fresh weight) of the whole root system was used to estimate percentage of AM root colonization. Sam-

ples were stained with 0.05% trypan blue in lactic acid [17] modified by the procedure described by Koske and Gemma [18]. The percentage of root colonization was determined using the grid-line intersect method [19]. Root segments were excised after clarifying and staining the roots, mounted on slides and observed under a light microscope.

Absolute responsiveness to mycorrhizas at the lowest P level, $R_{[18\text{ mg Olsen P}\cdot\text{kg}^{-1}]}$, was determined as described by Janos [7]. Following the same author, this parameter was then relativized as done by Plenchette *et al.* [20].

2.6. Statistical analysis

All data were analyzed by ANOVA. Means were compared by Tukey's multiple range test ($P \leq 0.050$). The analysis was performed using Systat[®] 7.0.1. (SPSS, Inc. © 1997).

3. Results

Overall, in our experiment, mycorrhization of both papaya and pineapple significantly favored plant development and nutritional status.

Mycorrhization of papaya plants resulted in significant increases in almost all growth parameters as compared with all phosphorus fertilization levels (*table I*), except for plants grown with $79.4\text{ mg Olsen P}\cdot\text{kg}^{-1}$, whose fresh root biomass was statistically indistinguishable from that of mycorrhizal plants. Significant increases in fresh biomass because of mycorrhization were detected as compared with the fresh lowest P level, being up to six times higher for root fresh weight and around 3.5 times higher for shoot weight. The highest significant difference in dry matter (up to 3.5 times) was also found after comparing mycorrhizal papayas with non-mycorrhizal ones at the lowest P fertilization level. In addition, mycorrhization significantly improved plant nutritional status (*table II*). Papaya plants inoculated with *G. mosseae* exhibited significantly higher shoot mineral contents of phosphorus and

Table I.

Effect of the inoculation of *Glomus mosseae* on the development of papaya plants cv. Sunrise, compared with increasing levels of phosphate fertilizers, 5 months after an AMF inoculation.

Available P in substrate (mg·kg ⁻¹)	Fresh weight (g)		Dry weight (g)
	Root	Shoot	Shoot
P _{18.3}	6.02 c	16.65 d	2.54 d
P _{48.0}	22.73 b	40.01 c	6.58 c
P _{79.4}	35.29 a	49.37 b	8.09 b
P ₁₀₀	27.07 b	43.07 c	7.36 bc
P _{18.3} + <i>G. mosseae</i>	36.66 a	56.64 a	9.29 a

Within each column, data followed by the same letter are not significantly different according to Tukey's test ($P \leq 0.050$).

Table II.

Effect of the inoculation of *Glomus mosseae* on the N, P and K contents of papaya plant cv. Sunrise shoots compared with increasing levels of phosphate fertilizers, 5 months after an AMF inoculation.

Available P in substrate (mg·kg ⁻¹)	Shoot nutrient content (mg/plant)		
	N	P	K
P _{18.3}	77.86 c	4.06 e	61.54 d
P _{48.0}	168.68 a	9.77 d	130.24 c
P _{79.4}	138.00 b	15.29 b	179.08 b
P ₁₀₀	139.85 b	12.96 c	144.87 c
P _{18.3} + <i>G. mosseae</i>	146.10 b	18.95 a	228.28 a

Within each column, data followed by the same letter are not significantly different according to Tukey's test ($P \leq 0.050$).

potassium than those without mycorrhizas at every P treatment. These increases were highest when compared with the lowest P level, *i.e.*, 4.7 and 3.7 times higher for P and K, respectively. In the case of nitrogen, mycorrhization significantly increased its contents as compared with P lowest level.

For pineapple, benefits derived from mycorrhization were less evident than those registered in papaya (*table III*). Mycorrhization significantly increased plant fresh biomass versus all P levels, but relative increases (up to 1.5 times) were lower than those for papaya. Otherwise, pineapple dry matter of mycorrhizal plants was identical to those plants grown in the P_{48.0} treatment,

but significantly higher than in the other P treatments. On the other hand, shoot nutrient contents of pineapple were less affected by mycorrhization than papaya (*table IV*). P mineral content of shoots was the only macroelement significantly increased by mycorrhizas as compared with all P levels.

Both papaya and pineapple crops exhibited mycorrhizal colonization of roots, although papaya roots had a greater percentage of root length colonized than pineapple (21%) (*table V*). Absolute responsiveness to the symbiosis at P_{18.3} showed significant differences depending on the crop, being highest for papaya plants $R_{[18 \text{ mg Olsen P} \cdot \text{kg}^{-1}]} = 6.75$, while the value for

Table III.

Effect of the inoculation of *Glomus mosseae* on the development of pineapple plants cv. Smooth Cayenne, compared with increasing levels of phosphate fertilizers, 7 months after an AMF inoculation.

Available P in substrate (mg·kg ⁻¹)	Fresh weight (g)		Dry weight (g)
	Root	Shoot	Shoot
P _{18.3}	17.21 b	166.07 b	20.51 b
P _{48.0}	15.02 b	162.97 b	20.88 ab
P _{79.4}	14.38 b	156.46 b	18.93 b
P ₁₀₀	16.17 b	149.42 b	19.14 b
P _{18.3} + <i>G. mosseae</i>	21.00 a	187.36 a	23.48 a

Within each column, data followed by the same letter are not significantly different according to Tukey's test ($P \leq 0.050$).

Table IV.

Effect of the inoculation of *Glomus mosseae* on the N, P and K contents of pineapple plant cv. Smooth Cayenne shoots compared with increasing levels of phosphate fertilizers, 7 months after an AMF inoculation.

Available P in substrate (mg·kg ⁻¹)	Shoot nutrient content (mg/plant)		
	N	P	K
P _{18.3}	156.14 a	8.91 b	735.37 a
P _{48.0}	149.36 ab	9.61 b	629.23 bc
P _{79.4}	132.63 ab	8.79 b	611.23 bc
P ₁₀₀	129.44 b	8.81 b	566.50 c
P _{18.3} + <i>G. mosseae</i>	151.26 ab	19.68 a	681.59 ab

Within each column, data followed by the same letter are not significantly different according to Tukey's test ($P \leq 0.050$).

pineapple was 2.97 (table V). The relative responsiveness was 72.60 for papaya and 12.65 for pineapple.

4. Discussion

Our results confirm the ability of both papaya and pineapple crops to establish mycorrhizal symbiosis, *i.e.*, mycotrophy, which has previously been reported by other authors [10–13]. Soils from tropical regions destined for agriculture are normally constrained by several factors such as a low nutrient capital, moisture stress, ero-

sion, high P fixation, high acidity with aluminum toxicity, and a low soil biodiversity [8]. These unfavorable conditions may be responsible for both crops being naturally adapted to forming this beneficial plant-microbe association.

In our experiment and for both crops, mycorrhization resulted in benefits higher than those derived from any of the P treatments. However, the magnitude of response was different when comparing both plant species. Phenomena involved in the interaction between plants and mycorrhizal fungi have been widely studied and defined by numerous authors throughout

Table V.

Mycorrhizal responsiveness and root colonization percentage for papaya and pineapple plants at the end of the experiment, 5 months after an AMF inoculation for papaya plants and 7 months for pineapple.

Plant species	Mycorrhizal responsiveness		Root colonization (%)
	Absolute ¹ R _[18.3]	Relative ^{1,2} (%)	
Papaya	6.75	72.60	63.00
Pineapple	2.97	12.65	21.00

¹ According to the definition described by Janos [7].

² Following the formula described by Plenchette *et al.*, [20].

the last decades [7]. The last review available on this topic established two main concepts to explain mycorrhizal symbiosis: dependence and responsiveness. Mycorrhizal dependence, a property which relies on the plant genotype, is defined as the ability of plants to grow without mycorrhizas [7]. In contrast, responsiveness to the symbiosis refers to the magnitude of growth response due to mycorrhization and can be considered as a conjoint property of a plant-fungus interaction [7]. Otherwise, although dependence and responsiveness, as previously defined, may be correlated, they are somewhat independent [7].

In our experiment, both the P fertilization levels and fungus isolate were identical for both crops: thus, differences detected between them could only be attributed to plant species. In the absence of mycorrhizas and at the lowest P level, pineapple can grow better than papaya. According to Janos [7], that may suggest that papaya plants are more dependent on mycorrhizas. In addition, our data show a higher responsiveness (absolute and relative) for papaya plants which seems to be correlated with higher fungal root colonization than for pineapple. These differences between crops must be taken into account when inoculating. Therefore, we recommend screening to determine the most suitable plant-fungi interaction to optimize the process.

The use of AMF as a key ingredient within low input production systems has previously been proposed [21]. The results from our experiment indicate that benefits

derived from mycorrhization may replace P fertilization and, therefore, this symbiosis can be seriously considered as a way to reduce P inputs during the nursery phase for commercial production systems. Papaya and pineapple production systems currently used in the Canary Islands do not include mycorrhization in the nursery phase. Our results show that the application of this beneficial plant-microbe association may contribute to improving the plant production process. Nevertheless, as has been shown herein, a good knowledge of the mycorrhizal properties of the host plant is recommended for an optimal inclusion of this biotechnology for commercial purposes.

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La micorrización temprana reduce los aportes de fertilización fosforada durante la fase de vivero en dos cultivos tropicales, papaya (*Carica papaya* L.) y piña [*Ananas comosus* (L.) Merr.].

Resumen — Introducción. El uso de hongos formadores de micorrizas como biofertilizantes puede reducir los insumos químicos en vivero, permitiendo obtener plantas de alta calidad con un menor aporte de abonos. Sin embargo, una de las mayores dificultades para la aplicación sistemática de esta biotecnología reside en la ausencia de un conocimiento profundo de la respuesta a la simbiosis micorrícica de muchos cultivos. En nuestro trabajo, se evalúa el efecto de la micorrización temprana en papaya y piña, como alternativa a los programas rutinarios de fertilización fosforada durante la fase de vivero. **Material y métodos.** Las plántulas de papaya y los brotes de piña se inocularon con el aislado micorrícico *Glomus mosseae* y se cultivaron sobre sustratos enriquecidos con cantidades crecientes de P soluble. A los 5 y 7 meses después de la inoculación (papaya y piña, respectivamente), se registraron los valores correspondientes a desarrollo y estado nutricional. **Resultados.** Para ambos cultivos, los beneficios derivados de la micorrización tanto en desarrollo como en estado nutricional fueron significativamente superiores a los derivados de la aplicación de P soluble. Así, independientemente de la cantidad de P aplicado, las papayas micorrizadas presentaron valores de biomasa y de contenido foliar en macronutrientes significativamente mayores que las no micorrizadas. En el caso de la piña, el efecto observado al nivel más bajo de P, resultó ser de gran importancia en términos de desarrollo y contenido foliar de fósforo. **Conclusión.** La diferencia en magnitud de los beneficios observados parecen estar correlacionados con las exigencias específicas de P para cada cultivo. Nuestro trabajo pone de relieve las ventajas potenciales de la micorrización temprana durante la fase de vivero como alternativa sostenible para reducir el uso de abonos fosforados en los sistemas de producción vegetal.

España / *Carica papaya* / *Ananas comosus* / estado juvenil de las plantas / aplicación de abonos / abonos fosfatados / biofertilizantes

