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Effects of a network of mycorrhizae on capsicum (*Capsicum annuum* L.) grown in the field with five rates of applied phosphorus

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Abstract. This field trial determined the importance of mycorrhizae [*Acaulospora mellea* Spain & Schenck, *Gigaspora margarita* Becker & Hall, *Glomus clarum* Nicolson & Schenck, *Glomus etunicatum* Becker & Gerdemann, and *Scutellospora pellucida* (Nicol. & Schenck) Walker & Sanders], established from an existing intact network of vesicular-arbuscular mycorrhizae (VAM) propagules, for production of capsicum (*Capsicum annuum* L. cv. Target) in a low phosphorus (≤14 mg NaHCO3-extractable P/kg) Typic Paleudalf. The mycorrhizal network was formed previously with sweetcorn (*Zea mays* L. cv. Snosweet) plants grown in distinct rows. A narrow band of milled superphosphate was applied at 0 (P_1), 5 (P_2), 15 (P_3), 45 (P_4), or 135 (P_5) kg P/ha to plots that were either fumigated (VAM–) or not fumigated (VAM+).

The higher ($P < 0.05$) concentrations of P in the youngest mature leaf (blade plus petiole) of VAM+ than those of VAM– capsicum plants at P_1, P_2, and P_3 coincided with a greater ($P < 0.05$) weight of marketable fruit of VAM+ than of VAM– plants; this finding confirmed the importance of VAM to the enhanced P nutrition of capsicum at low P levels. In the non-fumigated soil (1061 non-dormant infective VAM propagules/g air-dry soil), the inverse sine transformed means of percentage colonisation of roots were generally unaffected by P application, indicating that addition of P may not reduce VAM colonisation of roots if the inoculum potential of the soil is high. An alternative hypothesis to account for the relatively undiminished mycorrhizal colonisation of VAM+ plants at high P rates may relate to a reduction in colonisation for roots growing within the narrow band of applied P, but not for roots growing in the much larger volume of soil outside of this localised P zone. The absence of reduced yields and of lower starch concentrations of roots of VAM+ relative to VAM– plants suggested that photosynthate production was surplus to the requirements of the plant and fungus for the irradiance encountered during the trial. The gross margin for VAM– plants was maximal at P_5 ($AU3340/ha), and this amount was similar to the margin for VAM+ plants grown at all treatments except P_1, which had a lower gross margin. As a substitute for P, mycorrhizae have limited potential in intensive vegetable production systems since the cost of P is low compared with total costs. However, other benefits of VAM such as decreased susceptibility to disease and improved structure of the soil need to be fully assessed to determine the full benefit of mycorrhizae in such systems.

Introduction

Soil beds that are fitted with trickle irrigation tubing and covered with plastic mulch film are sometimes re-used for a second crop by growers in the Bowen (R. M. Wright, pers. comm.) and Bundaberg districts of Queensland. Once harvested, plant tops of the first crop [such as capsicum and tomato (*Lycopersicon esculentum* Mill.)] are slashed and the undisturbed beds are sown or transplanted with a second crop [such as sweetcorn or pumpkin (*Cucurbita pepo* L.)]. The primary motivation for this practice is to extend the life of the plastic mulch film and trickle tubing and to maximise the recovery of residual fertiliser from the first crop. However, the method also lends itself to the development of a network of interconnecting vesicular-arbuscular mycorrhizae (VAM) propagules,

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including an extensive mycelial web, which may greatly benefit the second crop. The benefit of mycorrhizae, established from an existing intact hyphal network, on the dry matter yield of capsicum and tomato plants sown into this system was demonstrated in greenhouse experiments conducted by Olsen *et al*. (1999), particularly at low rates of applied phosphorus (<9.2 mg P/kg). However, a yield depression of VAM+ relative to VAM– plants at higher P rates was accompanied by lower starch concentrations measured in the roots of the mycorrhizal plants. Olsen *et al*. (1999) suggested that this yield depression of VAM+ relative to VAM– plants may have been a result of the relatively low light levels within the greenhouse (light transparency of the roof was 66%), with the photosynthate production of VAM+ plants insufficient to meet the carbon (C) demand of both host and endophytes. It is also plausible that some other phenomenon (e.g. high temperatures in the greenhouse or restricted root volume in the pots) may have been the cause. Under field conditions, where light levels may be appreciably higher than in the greenhouse and where high temperatures and restricted root volumes may be avoided, the benefits of VAM may not be abated by the C-drain of the endophytes.

Information is relatively sparse on the function of mycorrhizae in field environments (Bagyaraj and Varma 1995), and the field trials that have been conducted show variable plant responses (Fitter 1985). Indeed, Marschner (1995) stated that the major limitation for predictions on the effects to be expected from inoculation with VAM is our poor knowledge of the functioning of the associations under field conditions. Furthermore, Marschner (1995) suggested that it seems more promising under most circumstances to manipulate the inoculum potential of the indigenous VAM indirectly by soil management and crop rotation than by the addition of VAM inoculum directly to the soil.

The present experiment was conducted to determine the importance of VAM for vegetable production in the field environment; a capsicum crop was grown in soil in which mycorrhizal propagules (either live or killed) had been established by a previous crop of sweetcorn and to which 5 rates of P were applied. The study also further investigated the findings and hypotheses developed from the greenhouse experiments conducted by Olsen *et al*. (1999).

Materials and methods

A field trial was conducted primarily to assess the effects of mycorrhizae, established from an existing intact network, on the growth response of capsicum cv. Target plants at 5 rates of P. The trial involved 3 distinct phases. In the first (preparation) phase, sorghum cv. Jumbo was grown in soil (previously cropped with sugarcane hybrid Q110 from September 1988 to July 1993) to augment the number of naturally occurring VAM propagules at the site and to deplete the soil of P.

Following removal of the tops of the sorghum plants and cultivation of the soil, sweetcorn cv. Snosweet was grown in the second (preconditioning) phase to establish a mycorrhizal network within distinct rows and to deplete the soil of P further. In the third (production) phase, capsicum cv. Target seedlings were transplanted into either fumigated (VAM–) or unfumigated (VAM+) sections of the soil beds which were previously cropped with sweetcorn. A schedule of operations for the trial is shown in Table 1.

Site description

The field trial site (24°58′11.6″S, 152°24′25.0″E) was located approximately 13 km SSE of Bundaberg. The soil is variously classified as a Typic Paleudalf (USDA 1975) and a Bleached-Sodic Mesotrophic Yellow Dermosol (Isbell 1996).

Soil cores (diameter 40 mm, depth 60 cm) were taken from 4 positions within the designated production crop area of the field trial (viz. 12, 24, 36, and 48 m from the designated eastern boundary) on 5 January 1995; the soil in each core was separated into 4 depths (0–10, 10–20, 20–40, and 40–60 cm) and air-dried, and chemical (Table 2) and physical properties were then determined for each of the 16 subsamples. Using the texture grades provided by Northcote (1979), the soil is described as a sandy loam in the top 40 cm, becoming a sandy clay loam in the 40–60 cm zone.

Preparation phase

In the preparation phase, a sorghum cover crop was grown at the field site on 0.38 ha (32 by 120 m) of cultivated land in which sugarcane was previously grown. Overhead irrigation water was applied throughout the crop cycle to supplement rainfall and ensure that a satisfactory growth rate was attained. Prior to the first harvest (Table 1), the tops of the sorghum plants within 6 randomly placed 1-m^2 quadrats were cut at ground level on 17 February 1994, placed in labelled hessian bags, dried in a tobacco barn at 65°C for 4 days, and weighed. The remaining tops of the sorghum cover crop were then cut off at ground level, and after the tops were raked off, the new shoots were allowed to regrow. Tops were again cut and raked off prior to cultivation of the soil and formation of beds (Table 1). Soil ameliorants were applied to the soil at a rate of 5 t/ha prior to (gypsum), during (dolomite), and after (dolomite) the sorghum crop. The following elements (kg/ha) were also applied (broadcast or sprayed onto the ground) during the preparation phase: 100 N, 300 K, 206 S, 123 Ca, 40 Mg, 2 Cu, 10 Zn, 5 Fe, 48 Mn, 9 B, and 1 Mo.

On 23 January 1994 and again on 24 June 1994, sorghum roots were sampled from approximately 20 soil cores (diameter 20 mm, depth 10 cm) at random positions, so that a cursory inspection of the cleared and stained roots (Koske and Gemma 1989) would give an indication of the prevalence of colonising VAM hyphae.

At the end of the preparation phase, soil beds (1.36 m between centres) were formed (Table 1) into 18 rows of length 120 m, running in an E–W direction. Rows were arranged into 3 sets of 6, with adjacent sets separated by a 1.64-m spray-track. Polyethylene trickle irrigation tubing (wall thickness 200 μm, internal diameter 16 mm, emitter spacing 300 mm) was laid along the centre of each bed and then covered with 25-μm white polyethylene plastic mulch film (1.2 m wide).

Preconditioning phase

Two rows of sweetcorn seeds were sown (Table 1) at a depth of 30 mm into each bed (one each side of the trickle irrigation tubing) with a precision air-seeder (38-cm inter-row spacing, 35-cm intra-row spacing); this planting arrangement was equivalent to 42 000 plants/ha. Chlorinated irrigation water (residual Cl of 1 mg/L) was applied to maintain tensiometer suction in the root-zone (0–40 cm) between 10 and 50 kPa. Soluble fertilisers were introduced into the irrigation water (fertigation) to supply the following elements (kg/ha): 120 N, 146 K, 117 S, 24 Ca, 40 Mg, 7 Zn, and 6 Mn. The contact herbicides diquat and paraquat were applied at standard rates on 2 occasions during the preconditioning phase to control weeds.

The position of plots intended for capsicum plants to be grown in the production phase was ascertained from stringlines which were run

Table 1. Summary of the sequence of operations in the field trial

Task description	Date performed
Preparation phase (sorghum)	
Soil deep ripped and rotary hoed	15 Oct. 1993
Sorghum cv. Jumbo seed broadcast at 18 kg/ha	12 Nov. 1993
Sorghum tops cut and raked off (new shoots allowed to regrow)	25 Feb. 1994
Sorghum tops cut and raked off	16 Sept. 1994
Soil deep-ripped	27 Sept. 1994
Soil rotary hoed	3 Oct. 1994
Soil beds formed, trickle tubing and white plastic mulch film laid	10 Oct. 1994
Preconditioning phase (sweetcorn)	
Sweetcorn cv. Snosweet seeds sown with an air seeder (2 rows per bed)	9 Nov. 1994
Tops of 10 of the 34 sweetcorn plants per plot (6 m by 1.36 m) harvested for a uniformity assay	19–20 Jan. 1995
Remaining sweetcorn tops cut off at ground level and removed	24 Jan. 1995
White plastic mulch film and trickle tubing removed and discarded	30 Jan. 1995
Potassium nitrate fertiliser applied as a narrow band to all plots	9 Feb. 1995
Soil in bed centres sliced with a plate of steel to make a narrow furrow; a mixture of superphosphate and sand poured into the furrow to give 1 of 5 P rates per plot (0, 5, 15, 45, or 135 kg P/ha)	10 Feb. 1995
New trickle tubing and white plastic mulch film laid over the original soil beds in which the sweetcorn was grown	28 Feb. 1995
Soil of VAM– plots fumigated	8 Mar. 1995
Production phase (capsicum)	
Capsicum cv. Target seedlings transplanted (originally sown into seedling trays on 4 Jan. 1995)	20 Mar. 1995
First fruit harvest	22 June 1995
Second fruit harvest	6 July 1995
Third fruit harvest	13 July 1995
Fourth fruit harvest	27 July 1995
Fifth (and final) fruit harvest	10 Aug. 1995
Tops of capsicum plants cut off at ground level for dry weight determination	14 Aug. 1995
Roots and adhering soil from 3 randomly selected root systems per plot exhumed for VAM, root length, dry weight, and starch determinations	16 Aug. 1995

between permanent pegs placed at the perimeter of the field site. Of the 34 sweetcorn plants (2 rows of 17 plants) growing within each designated plot (6 by 1.36 m), the tops of 10 (the 1st, 5th, 9th, 13th, and 17th plant in each row) were cut at ground level (Table 1), placed in labelled hessian bags, dried in a tobacco barn at 65°C for 11 days, and weighed. All the remaining sweetcorn plants were severed at ground level with cane knives and removed and the plastic mulch film and trickle tubing were removed and discarded (Table 1).

Approximately 200 g of field soil and adhering sweetcorn roots (0–15 cm) were sampled on 21 February 1995 from each of 20 randomly selected positions within the trial site designated for the production crop, air-dried in a cool, dark position, and thoroughly mixed. Approximately 500 g of the air-dried material was sent to the International Collection of Arbuscular and Vesicular-arbuscular Mycorrhizal Fungi (INVAM) at West Virginia University, USA (Morton *et al.* 1993), where it was incorporated into the collection and given the accession code 'AU405'. The VAM fungi identified in the inoculum were *Acaulospora mellea*, *Gigaspora margarita*, *Glomus clarum*, *Glomus etunicatum*, and *Scutellospora pellucida*.

A most probable number (MPN) test (Porter 1979) using sequential 2-fold dilutions ranging from 1 : 250 to 1 : 128 000 and sweetcorn as the bioassay crop was conducted on the soil sampled from the field on 21 February 1995. Standard MPN statistics were used to calculate the number of propagules in each cell of undiluted inoculum (Daniels and Skipper 1982).

Following removal of the plastic mulch film and the trickle tubing, a narrow band of potassium nitrate fertiliser (depth 75 mm) was applied to all plots (285 kg fertiliser/ha which supplied 37 kg N/ha) approximately 75 mm from the centre of each bed (Table 1). The next day (Table 1), the centre of each plot was cut to a depth of approximately 75 mm with a sharpened steel plate so that a narrow band of milled superphosphate (9.0% P) could be applied at 0 (P_1), 5 (P_2), 15 (P_3), 45 (P_4), or 135 (P_5) kg P/ha. Following the laying of trickle irrigation tubing and covering with white plastic mulch film, soil in the VAM– plots was fumigated using the hot gas method with a mixture of 98% methyl bromide (CH_3Br) and 2% chloropicrin (CCl_3NO_2) at 721 kg/ha.

Production phase

Capsicum seedlings (cv. Target) that were found to be uncolonised by VAM were transplanted into the field (Table 1) into 26-plant plots arranged in a randomised blocks layout. Five P rates were applied in full factorial combination with 2(+/–) VAM; all 10 combinations were replicated in 4 blocks. The 26 capsicum seedlings were transplanted 220 mm apart and the bed centres were spaced 1.36 m apart, resulting in a population of 33 422 plants/ha. The 3 plants at each end were designated as buffer plants, resulting in 20 datum plants per plot.

The following elements (kg/ha) were administered to the capsicum crop grown in the production phase: 304 K in a band; ≥ 122 S, ≥ 46 Ca, 30 Mg, 4 Zn, 4 Mn by fertigation; and 0.3 B and 0.6 Mo as separate foliar

Table 2. Chemical analysis of the Typic Paleudalf (13 km SSE of Bundaberg) at various depths prior to the production phase of the field trial

The value at each depth is the mean of 4 cores (diameter 40 mm) sampled from the field trial site on 5 January 1995. The range of values from these cores at each sample depth is presented in parentheses following the mean

Property	Unit of measurement	Soil depth (cm) 0–10	10–20	20–40	40–60	Desirable range[A]	Method	Reference(s)
pH		6.8 (6.7–7.0)	6.3 (6.1–6.5)	5.9 (5.7–6.0)	6.0 (5.4–6.2)	6.0–7.0	1 : 5 soil : water	Loveday (1974)
Elec. conductivity	dS/m	0.12 (0.04–0.22)	0.18 (0.06–0.30)	0.09 (0.04–0.14)	0.07 (0.04–0.12)	<0.30	1 : 5 soil : water	Bower and Wilcox (1965)
Organic carbon	%	1.1 (0.9–1.3)	1.0 (0.9–1.2)	0.6 (0.5–0.6)	0.4 (0.4–0.4)	>2.0	$K_2Cr_2O_7 + H_2SO_4$	Walkley and Black (1934); Sims and Haby (1971)
NO_3-N	mg/kg	2 (2–2)	2 (2–2)	2 (2–2)	2 (2–2)	25–60	1 : 5 soil : water	Bremner (1965)
P	mg/kg	14 (12–16)	11 (9–15)	3 (2–4)	2 (2–2)	60–100	1 : 100 soil : 0.5 M $NaHCO_3$	Colwell (1963)
K	cmol(+)/kg	0.12 (0.08–0.16)	0.07 (0.07–0.08)	0.05 (0.04–0.05)	0.05 (0.04–0.06)	0.37–1.5	1 : 20 soil : 1 M NH_4Cl, pH 7.0	Tucker (1971); Loveday *et al.* (1972)
Ca	cmol(+)/kg	2.95 (2.00–3.80)	2.60 (1.60–3.20)	1.01 (0.83–1.30)	0.73 (0.61–0.77)	>3.0	1 : 20 soil : 1 M NH_4Cl, pH 7.0	Tucker (1971); Loveday *et al.* (1972)
Mg	cmol(+)/kg	1.08 (0.94–1.30)	0.77 (0.58–0.98)	0.54 (0.38–0.82)	1.35 (1.10–2.00)	>0.4	1 : 20 soil : 1 M NH_4Cl, pH 7.0	Tucker (1971); Loveday *et al.* (1972)
Na	cmol(+)/kg	0.18 (0.08–0.25)	0.19 (0.11–0.26)	0.11 (0.08–0.15)	0.21 (0.14–0.24)	<2.0	1 : 20 soil : 1 M NH_4Cl, pH 7.0	Tucker (1971); Loveday *et al.* (1972)
CEC[B]	cmol(+)/kg	4.33 (3.12–5.47)	3.62 (2.37–4.51)	1.70 (1.37–2.02)	2.33 (1.91–3.02)	>4.0	1 : 20 soil : 1 M NH_4Cl, pH 7.0	Tucker (1971); Loveday *et al.* (1972)
Fe	mg/kg	42 (29–58)	49 (36–72)	21 (15–25)	9 (6–12)	>2.0	1 : 2 soil : 0.005 M DTPA	Lindsay and Norvell (1978)
Cu	mg/kg	0.5 (0.4–0.7)	0.5 (0.3–0.7)	0.1 (0.1–0.1)	0.1 (0.1–0.1)	0.3–10	1 : 2 soil : 0.005 M DTPA	Lindsay and Norvell (1978)
Mn	mg/kg	2 (1–3)	1 (1–1)	0 (0–0)	0 (0–0)	4–45	1 : 2 soil : 0.005 M DTPA	Lindsay and Norvell (1978)
Zn	mg/kg	2.4 (1.9–3.4)	3.4 (1.1–10.0)	0.6 (0.1–1.8)	0.4 (0.1–0.7)	1–10	1 : 2 soil : 0.005 M DTPA	Lindsay and Norvell (1978)
Cl	mg/kg	30 (7–52)	67 (6–119)	14 (6–25)	19 (10–34)	<300	1 : 5 soil : water	Rayment and Higginson (1992)
SO_4-S	mg/kg	49 (6–112)	90 (23–155)	61 (24–97)	76 (54–90)	20–100	1 : 5 soil : 0.01 M $Ca(H_2PO_4)_2$	Fox *et al.* (1964); Barrow (1967); Beaton *et al.* (1968)
B	mg/kg	1.1 (0.9–1.4)	0.7 (0.5–0.8)	0.4 (0.3–0.5)	0.4 (0.3–0.6)	2–5	1 : 2 soil : hot 0.01 M $CaCl_2$	Cartwright *et al.* (1983)

[A]Incitec (1989).

[B]Cation exchange capacity estimated as the sum of Na, Ca, K, Mg.

sprays. The elements Ca and S were supplied in increasing amounts for the P_2, P_3, P_4, and P_5 treatments from the addition of superphosphate (20% Ca, 11% S). Nitrogen was supplied to all plots as one basal application of potassium nitrate prior to planting (see above), as 9 fertigations of calcium nitrate (total 37.5 kg N/ha), and as 18 fertigations with urea (total 112.5 kg N/ha) during the life of the crop.

The following pesticides were applied at standard rates: *Bacillus thuringiensis*, endosulfan, and methomyl for lepidopterous insects; $Cu(OH)_2$ for bacterial spot (*Xanthomonas campestris* pv vesicatoria); pirimicarb for green peach aphid [*Myzus persicae* (Sulzer)]; propargite for 2-spotted mite (*Tetranychus urticae* Koch); and diquat and paraquat for weeds. Sulfur was also applied for both bacterial spot and 2-spotted mite control.

The nitrate concentration in sap expressed from the petioles of the youngest mature leaves was measured at regular intervals by rapid colorimetric analysis (Merckoquant test strips analysed with a Nitracheck nitrate meter) to monitor the N status of the crop. The rate and frequency of fertigation with calcium nitrate and urea were varied during the life of the crop in an attempt to maintain petiole sap nitrate concentrations of plots within, or above, the range reported by Olsen and Lyons (1994) to be associated with 95 and 100% of maximum marketable fruit yield for a capsicum crop grown in autumn.

Temperature probes and an irradiance sensor installed adjacent to the trial area recorded a mean soil temperature (50 mm depth) of 18.7°C (range 8.4–28.3°C), a mean air temperature of 18.6°C (range 3.9–30.6°C), and a mean irradiance of 12.1 MJ/m^2. day (range 3.0–20.9 MJ/m^2. day) for the period 2 April–10 August 1995.

Three plants were selected in each plot for measurement of plant height (distance from the cotyledonary node to the terminal bud); the same 3 plants were measured 7, 14, 21, 35, and 49 days after transplanting (DAT).

The youngest mature leaf blade plus petiole (YML) was sampled from every second datum plant within each plot at 32, 43, and 50 DAT, corresponding to first anthesis, 80% flowering, and fruit set, respectively. The sampled index leaves were immersed and gently agitated in a 1 : 40 solution of surfactant : tap water; the surfactant (Extran 300) did not contain P. The samples were removed from this solution after 1 min and then immersed and gently agitated in clean tap water for approximately 20 s, followed by several rinses with deionised water. Washed samples were placed separately in labelled paper bags which were placed in a forced-draught oven at 65°C until the leaves were dry. The oven-dried leaves were ground through a 1-mm mesh in a stainless steel mill. Samples were dried again at 85ºC for 48 h before the measurement of the P concentration by HNO_3 digestion and inductively coupled plasma emission spectrometry (Zarcinas *et al.* 1987).

The root system of a buffer plant exhumed at each of the 3 leaf samplings was washed, blotted dry with paper towels, and cut into approximately 10-mm lengths. A sample of approximately 1 g of randomly selected root pieces was taken from each root system for VAM determination and placed in 70% ethanol until processing. Sampled roots were cleared and stained using the methodology of Koske and Gemma (1989) modified slightly, as described in Olsen *et al*. (1999), to improve the resolution between the root tissues and internal mycorrhizal structures. The proportion of the length of roots colonised by VAM of the total root length (expressed as a percentage) was determined by the gridline intersect method (Ambler and Young 1977), observing 100 root intersections under a dissecting microscope (×30) to obtain a standard error of ±4% (Giovannetti and Mosse 1980).

Capsicum fruit were harvested from the 20 datum plants grown in each of the 40 plots at 94, 108, 115, 129, and 143 DAT (Table 1), then graded and weighed. Coloured fruit were harvested and considered marketable at >80 g in weight and if free from blemishes and deformation. Yield measurements from each harvest were added to give total yield values. Following the yield measurements at each harvest, 4 fruit were randomly selected and cut longitudinally into quarters, and all pieces were placed in a labelled paper bag in a forced-draught oven at 65°C until dry; the moisture content of these fruit was then determined.

Following cutting and removal of the plant tops, the severed stems of 3 of the 20 datum plants grown in each plot were randomly selected; then, the roots from these severed plants were carefully exhumed at 149 DAT (Table 1). Roots were washed, blotted dry with paper towels, and separated into coarse roots (≥2 mm diameter) or fine roots (<2 mm diameter); the coarse roots were then weighed and placed in labelled paper bags. Inspection of all washed roots revealed no *Meloidogyne* spp. galls in any plot. The fine roots subsample was cut into approximately 10-mm lengths and weighed, and 2 weighed samples (approximately 1 g each) of randomly selected root pieces were taken for VAM and root length determination and placed in 70% ethanol until processing. The remaining roots were placed in labelled paper bags in a forced draught oven at 65°C until dry. Total dry weight of the fine roots from each plot was estimated by the following formula: (dry weight of remaining fine roots × total fresh weight of fine roots)/(total fresh weight of fine roots – fresh weight of fine roots taken for VAM and root length assessment).

Dry coarse roots and fine root samples were ground separately through a 1-mm mesh in a stainless steel mill and analysed for starch using an enzymic–colorimetric procedure (Rasmussen and Henry 1990).

The total length of fine roots of plants grown in each plot was calculated after the length of a subsample was determined using a root length scanner (Comair). The procedures for assessment of VAM colonisation of roots have been previously described.

P-equivalent values (the additional P requirement of a VAM– plant to attain the same yield as a VAM+ plant at a given level of P application) were mathematically derived from Mitscherlich equations fitted to plots of the weight of marketable fruit and the rate of applied P for VAM+ and VAM– plants:

$$Y = a + be^{(-kX)}$$

where Y is the weight of marketable fruit at any level of P application (X), a is the limiting or asymptotic weight of marketable fruit, b is the constant for the particular soil–plant combination reflecting the responsiveness of the soil, and k is the slope parameter. These equations were selected because they are biologically sensible and they have been used previously by other workers (e.g. Abbott and Robson 1984) to describe the dry weight response of agricultural crops to applied P.

Statistical analysis

The 10 key treatments reported in this study form a factorial of 2 VAM levels by 5 P rates, all at 187 kg N/ha. In addition, 2 extra treatments (2 P rates in combination with VAM+ only at 112 kg N/ha) were incorporated into the design of the original field trial. Initially, the effects of treatments on the capsicum crop variables were tested by analysis of variance (ANOVA) on the full 12 treatments × 4 replicates design. A follow-up ANOVA was then conducted to test the interaction between VAM and P by apportioning these treatment differences into factorial contrasts, using the error mean squares and degrees of freedom from the full model.

ANOVA was used to test the effects of treatments on percentage VAM colonisation of roots and on length of roots colonised by VAM following inverse sine and square-root transformations, respectively. All treatment means were compared using the protected l.s.d. procedure operating at $P = 0.05$.

Economic analysis

Using the cultural practices employed in the field trial, a gross margin budget was performed on the marketable fresh fruit yield data obtained for each of the treatments used in the field trial. A complete listing of the assumptions used in the economic analysis is provided in Olsen (1998).

Results

Preparation phase

Prior to the first harvest of tops of the sorghum crop, the estimated dry matter yield was 8.4 t/ha. Although no estimation of yield was made prior to the second (final) harvest of tops, a visual comparison of the tops suggested that the biomass prior to the second cut was slightly greater than that of the first. Cursory examination of the cleared and stained sorghum roots sampled on 23 January 1994 and 24 June 1994 showed VAM colonisation of approximately 25 and 40%, respectively.

Preconditioning phase

There was appreciable variation in the dry weight of tops of sweetcorn plants harvested from the 40 plots (5.29–8.54 t/ha) prior to planting the capsicum seedlings in the production phase. The natural occurrence of 5 VAM species found in the soil was comparable with the 2–4 species reported by Abbott and Robson (1985) to be frequently found in any one Australian soil.

The MPN test conducted on soil sampled prior to the commencement of the production phase revealed 1061 non-dormant infective propagules/g air-dry soil. This population of infection units was high and was certainly adequate to ensure high rates of colonisation of the capsicum transplants.

Production phase

For the various parameters reported for capsicum plants grown in this study, the VAM × P interaction was significant ($P < 0.05$) in approximately 30% of cases, which is appreciably more than would be expected by random chance alone. Therefore, the VAM × P interaction was considered to be a real effect, and interaction means for the capsicum crop variables are presented throughout this study for consistency.

Plant height

In terms of plant height, all treatments except VAM– plants grown at P_1 (which displayed a linear response over time), showed a sigmoidal growth response curve. The greater ($P < 0.05$) height of VAM+ than of VAM– plants grown at P_1 was first measured at 35 DAT; thereafter the differences continued to increase. No differences were detected between VAM+ and VAM– plants grown at P_5 at any measuring time.

Concentration of phosphorus in the index tissue

For capsicum plants at mid-growth to early fruiting, the concentration of P in the YML at the lower end of the adequate (Piggott 1986) or normal (Weir and Cresswell 1993) range was selected as the critical concentration for deficiency (0.30%). The critical P concentration for deficiency is displayed in Fig. 1*a–c* as a dashed horizontal line.

Irrespective of the time of sampling, the concentration of P in the YML of VAM+ plants grown at P_1, P_2, and P_3 was higher ($P < 0.05$) than that of VAM– plants grown at the same P rates (Fig. 1). In addition, at 43 and 50 DAT, the P concentration in the YML of VAM+ plants grown at P_4 was also higher ($P < 0.05$) than that of VAM– plants grown at the same P rate. Concentrations of P within the YML of VAM+ plants were in excess of the critical concentration for deficiency, except for plants grown at P_1 at all 3 sampling times. For VAM– plants, index tissue P concentrations were above the critical value only at $\geq P_4$ at all 3 sampling times.

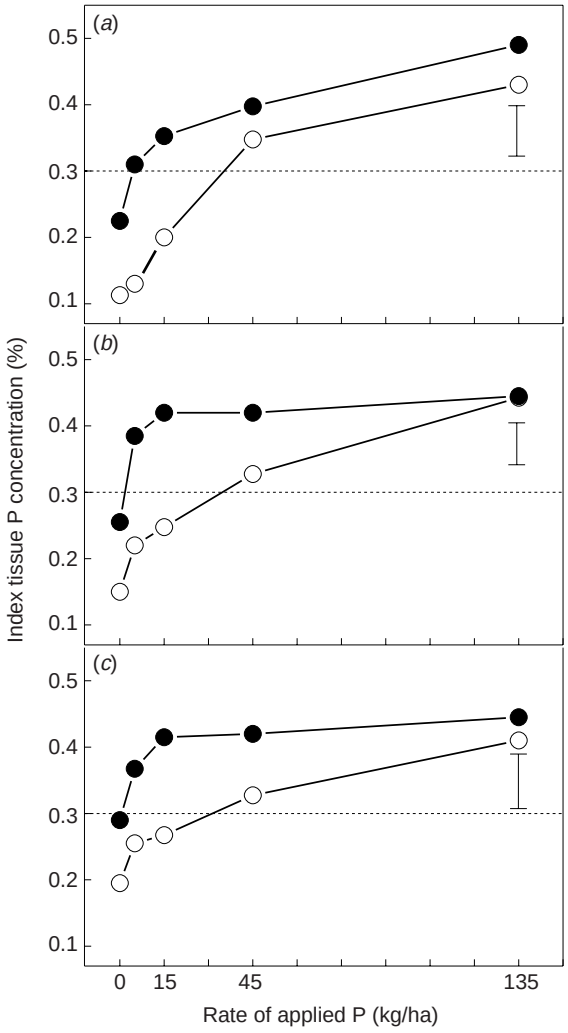

Fig. 1. Effect of applied P on the P concentration in the youngest mature leaf blade plus petiole (YML) of capsicum plants grown in the field trial at (*a*) 32 (first anthesis), (*b*) 43 (80% flowering), and (*c*) 50 (fruit set) days after transplanting. Plants were grown in the presence of a live mycorrhizal network (●) or a killed network (○). Vertical bars, representing the l.s.d. at $P = 0.05$, are for the comparison of means. Index tissue P concentration which is considered critical for deficiency appears as a horizontal dashed line.

Fresh fruit

The cumulative fresh weight of marketable fruit of VAM+ and VAM– plants grown at P_1 (the lowest P rate) and P_5 (corresponding with maximal fruit yields) is shown as a function

of time in Fig. 2. The cumulative fresh weight of marketable fruit harvested from plants grown at P_1 was greater ($P < 0.05$) for VAM+ than for VAM– plants at all harvests. Conversely, at P_5, the cumulative fresh weight of marketable fruit harvested from VAM+ and VAM– plants did not differ ($P > 0.05$) at any harvest time.

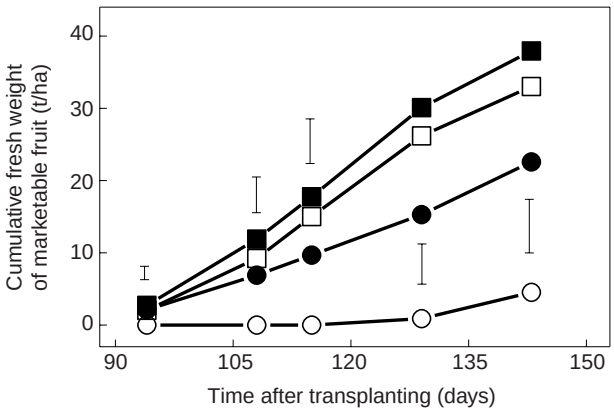

Fig. 2. Cumulative fresh weight of marketable fruit harvested over time from capsicum plants grown in the field trial. Plants were supplied with 2 rates of P (0 or 135 kg/ha; P_1 or P_5, respectively) in combination with a live (VAM+) or a killed (VAM–) mycorrhizal network: ○ P_1 VAM–; ● P_1 VAM+; □ P_5 VAM–; ■ P_5 VAM+. The ANOVA *F*-test for treatments was significant ($P < 0.05$) at each harvest. Vertical bars, representing the l.s.d. at $P = 0.05$, are for the comparison of means at each harvest.

The fresh weight of all fruit response curves for VAM+ plants tended to increase with applied P to approximately P_3 (Fig. 3*a*); at higher P rates, a yield plateau was attained. However, for VAM– plants, yields continued to increase with P application to approximately P_4; yields did not differ between P_4 and P_5. The fresh weight of all fruit of VAM+ plants grown at P_1, P_2, P_3, and P_4 was higher ($P < 0.05$) than that of VAM– plants grown at the same P rates.

The response curves for fresh weight of marketable fruit for VAM+ and VAM– plants (Fig. 3*b*) were similar to those for fresh weight of all fruit (Fig. 3*a*). The Mitscherlich equations fitted to these means in Fig. 3*b* were for the purpose of calculating P-equivalent values. The fresh weight of marketable fruit of VAM+ plants grown at P_1, P_2, P_3, and P_4 was higher ($P < 0.05$) than that of the VAM– plants grown at the same P rates.

The average fresh weight of individual marketable fruit of VAM+ plants was independent of P rate, whereas it increased in VAM– plants with an increase in P rate to approximately P_4 (Fig. 3*c*). The average fresh weight of individual marketable fruit of VAM+ plants grown at P_1, P_2, and P_3 was higher ($P < 0.05$) than that of VAM– plants grown at the same P rates.

The marketable fresh fruit weight ratio (the fresh weight of marketable fruit expressed as a percentage of the fresh weight of all fruit) for VAM+ plants did not vary among P rates, whereas for VAM– plants, this ratio continued to

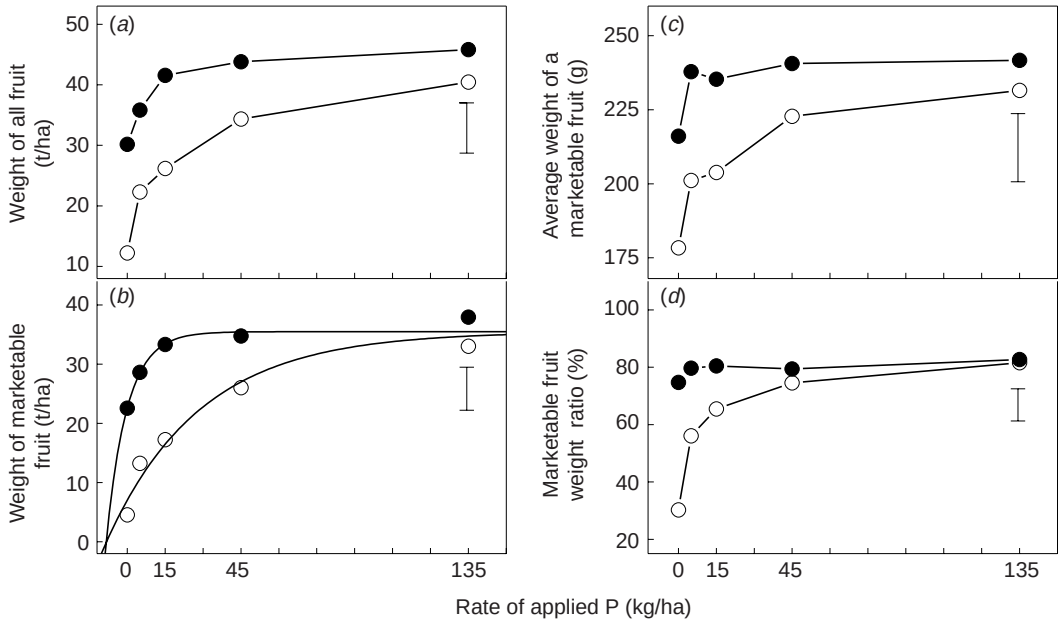

Fig. 3. Effect of applied P on the fresh weight of (*a*) all fruit and (*b*) marketable fruit and on (*c*) average fresh weight of individual marketable fruit and (*d*) marketable fresh fruit weight ratio for capsicum plants grown in the field trial. Plants were grown in the presence of a live (VAM+) mycorrhizal network (●) or a killed (VAM–) network (○). Vertical bars, representing the l.s.d. at $P = 0.05$, are for the comparison of means. In (*b*), Mitscherlich ($Y = a + be^{-kX}$) equations with a common asymptote were fitted to the VAM+ and VAM– means as follows:

VAM+ $Y = 35.5(\pm 1.4) - 12.9(\pm 2.8)\, e^{(-0.122\ (\pm 0.059)\ X)}$ ($R^2 = 0.95$)

VAM– $Y = 35.5(\pm 1.4) - 28.5(\pm 2.1)\, e^{(-0.027\ (\pm 0.006)\ X)}$ ($R^2 = 0.96$)

increase with P application up to approximately P_4 (Fig. 3*d*). The marketable fresh fruit weight ratio of VAM+ plants grown at P_1, P_2, and P_3 was higher ($P < 0.05$) than that of VAM– plants grown at the same P rates.

Root measurements

The dry weight of roots expressed as a percentage of the dry weight of the whole plant (root weight ratio) did not differ among treatments (Fig. 4*a*).

The length of fine roots for VAM+ plants did not vary among P rates, whereas for VAM– plants, this parameter increased with P application and attained a maximum at P_4, although values did not differ among P_3, P_4, and P_5 (Fig. 4*b*).

For the percent VAM colonisation of roots ($100 \times p$), an inverse sine transformation ($\sin^{-1}\sqrt{p}$) was performed on the data prior to ANOVA. With the exception of VAM+ plants grown at P_5 at 32 DAT, transformed means for mycorrhizal colonisation of VAM+ plants were greater ($P < 0.05$) than

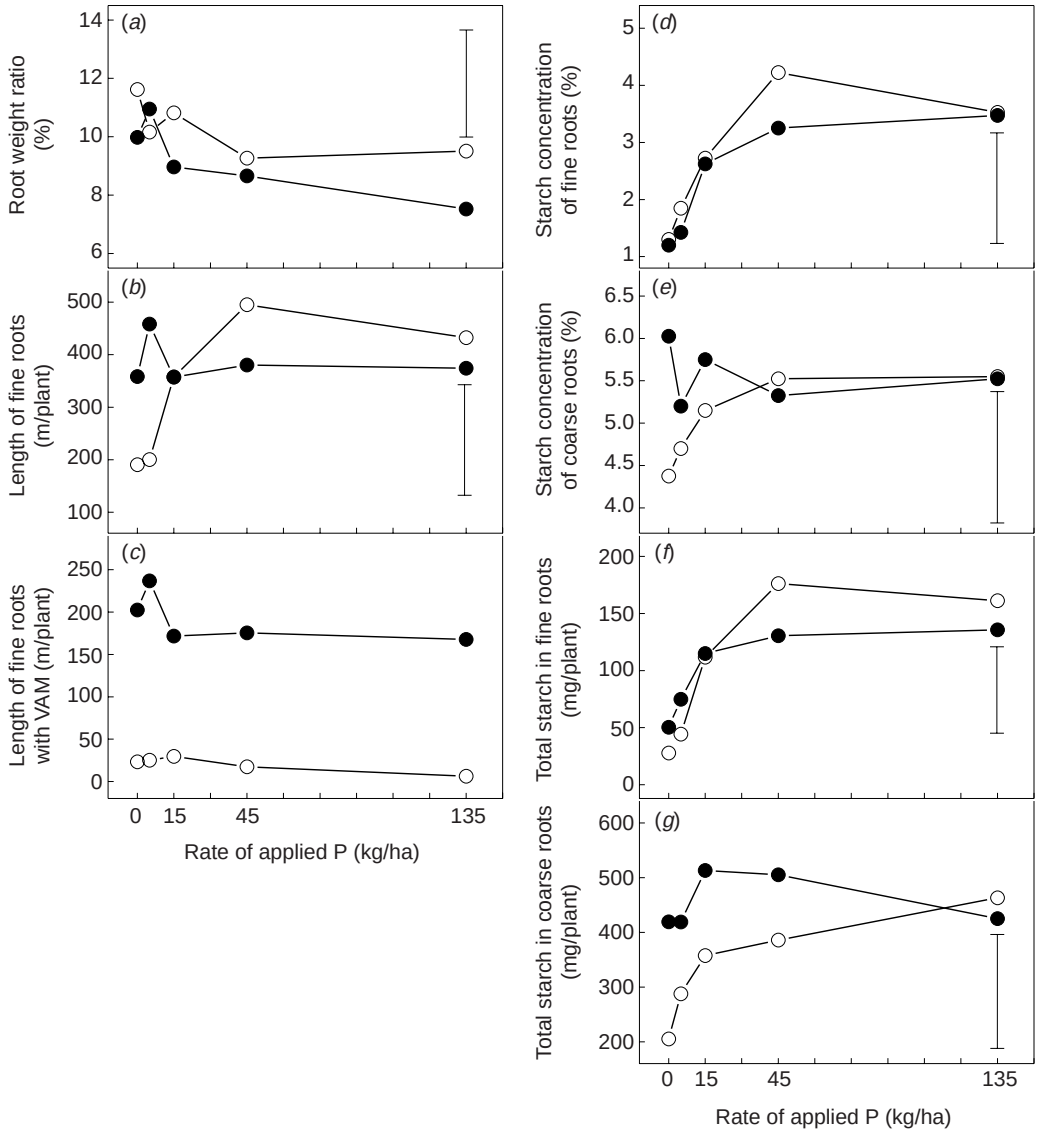

Fig. 4. Effect of applied P on (*a*) dry weight of roots expressed as a percentage of the dry weight of the whole plant (root weight ratio), (*b*) length of fine (<2 mm diameter) roots, (*c*) length of fine roots colonised by vesicular-arbuscular mycorrhizae (VAM), (*d*) starch concentration of fine roots, (*e*) starch concentration of coarse (≥2 mm diameter) roots, (*f*) starch content of fine roots, and (*g*) starch content of coarse roots of capsicum plants 149 days after transplanting into the field trial. Plants were grown in the presence of a live mycorrhizal network (●) or a killed network (○). In (*a*), (*d*), (*e*), and (*g*), the ANOVA *F*-test for treatments was not significant ($P > 0.05$). Vertical bars, representing the l.s.d. at $P = 0.05$, are for the comparison of means. In (*c*), back-transformed means (square-root transformation, $\sqrt{X + 0.5}$, where X is length of fine feeder roots per plant colonised by VAM) are presented; therefore, an l.s.d. value is not available for the back-transformed scale.

those of VAM– plants at 32, 43, 50, and 149 DAT (Table 3). At 149 DAT, the transformed means for mycorrhizal colonisation of the VAM– plants decreased ($P < 0.05$) with P application.

For the actual length of fine roots per plant colonised by VAM (X), a square-root transformation ($\sqrt{X + 0.5}$) was used. The square-root transformed means did not vary ($P > 0.05$) among the rates of P applied for each of the VAM+ or VAM– plants (data not presented). The square-root transformed means of VAM– plants were less ($P < 0.05$) than those of VAM+ plants for all treatment combinations (data not presented). The back-transformed means are presented in Fig. 4*c*, although an l.s.d. value is not available for the back-transformed scale.

For VAM+ and VAM– plants, the starch concentration of fine roots tended to increase with P application to approximately P_4 where a plateau was attained (Fig. 4*d*). The starch concentration of the coarse roots of VAM– plants tended to increase with P application, with maximum values attained at approximately P_4 and P_5, whereas concentrations for VAM+ plants remained relatively stable irrespective of P rate (Fig. 4*e*). However, pairwise comparisons could not be made for the starch concentration of fine or coarse roots because the ANOVA F-test for treatments was not significant ($P > 0.05$).

The total starch content of fine roots of VAM+ plants increased ($P < 0.05$) with P application; a plateau was attained at approximately P_3, although values did not differ at $\geq P_2$ (Fig. 4*f*). Similarly, total starch in fine roots of VAM– plants increased ($P < 0.05$) with P application, and a maximum value was attained at P_4; values did not differ at $\geq P_3$. At each individual rate of applied P, the total starch content of fine roots of VAM+ and VAM– plants did not differ. The total starch content of coarse roots of VAM– plants tended to increase with P application up to approximately P_5, whereas values for VAM+ plants tended to remain relatively stable, irrespective of P rate (Fig. 4*g*). However, pairwise comparisons could not be made because the ANOVA F-test for treatments was not significant ($P > 0.05$).

P-equivalent

For the relationship between fresh weight of marketable fruit and rate of applied P (Fig. 3*b*), high R^2 values for the VAM+ and VAM– means were attained by fitting Mitscherlich equations with a common asymptote. These Mitscherlich equations were fitted in Fig. 3*b* and revealed X-intercepts of –8.3 and –8.2 kg P/ha for the VAM+ and VAM– plants, respectively. As both curves approached the common asymptote of 35.5 t marketable fruit/ha, P-equivalent values progressively increased (Fig. 5). However, achievement of 95% of maximum yield of fresh marketable fruit required 87.0 kg/ha more P when plants were non-mycorrhizal than when they were mycorrhizal (Fig. 5).

Economic analysis

The response curves of gross margin for VAM+ and VAM– plants (Fig. 6) resembled those of fresh weight of marketable fruit (Fig. 3*b*); viz. an increase with applied P to approximately P_3, above which a yield plateau was attained (VAM+) and a continual increase with P application with a possible yield plateau at P_5 (VAM–). Marketable yield was a major determinant of gross margin, and the marketable yield for VAM– plants grown at P_5 (at which the yield was maximal for VAM– plants) did not differ ($P > 0.05$) from those of

Table 3. VAM colonisation of roots of capsicum plants at various times after transplanting into the field
Values at 32, 43, and 50 days after transplanting (DAT) are from the entire root systems of single buffer plants, whereas values at 149 DAT are the means of the VAM colonisation of the fine roots of 3 datum plants selected randomly from each plot. An inverse sine transformation [$\sin^{-1}\sqrt{p}$, where $100 \times p$ is the proportion of the length of roots colonised by VAM of the total root length (expressed as a percentage)] was performed on the data prior to ANOVA. Transformed means within a column followed by the same letter are not significantly different at $P = 0.05$ (F-test for treatments). Back-transformed data are in parentheses

Rate of applied P (kg/ha)	Time after transplanting (days) 32		43		50		149	
				VAM+				
0	0.20c	(3.9)	0.65b	(36.9)	0.73bc	(43.9)	0.86d	(57.9)
5	0.25c	(6.3)	0.64b	(36.0)	0.82bcd	(53.3)	0.82d	(53.3)
15	0.23c	(5.4)	0.67b	(38.5)	0.72bc	(43.4)	0.77d	(48.2)
45	0.20c	(4.1)	0.61b	(32.9)	0.72bc	(43.6)	0.78d	(49.2)
135	0.17bc	(2.9)	0.59b	(30.9)	0.62b	(34.0)	0.77d	(48.5)
				VAM–				
0	0.03a	(0.1)	0.04a	(0.1)	0.11a	(1.1)	0.36c	(12.5)
5	0.07ab	(0.5)	0.12a	(1.5)	0.16a	(2.6)	0.37c	(13.4)
15	0.03a	(0.1)	0a	(0)	0.04a	(0.2)	0.29bc	(8.3)
45	0.06a	(0.4)	0.06a	(0.4)	0.04a	(0.1)	0.18ab	(3.1)
135	0.08ab	(0.6)	0.11a	(1.1)	0.04a	(0.2)	0.13a	(1.7)
l.s.d. ($P = 0.05$)	0.11		0.14		0.20		0.13	

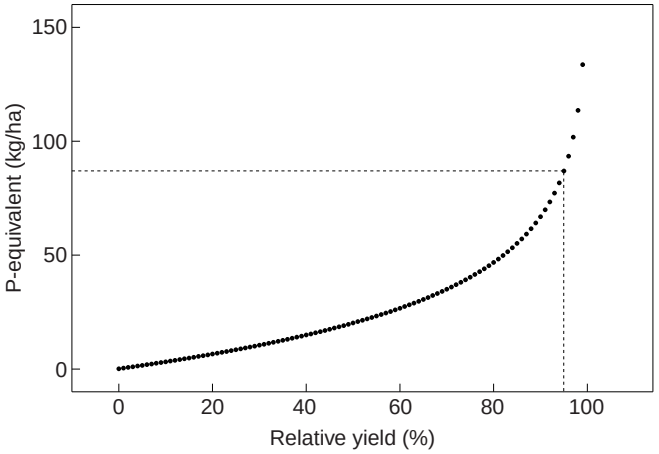

Fig. 5. P-equivalent values (the additional P requirement of VAM– plants to produce the same fresh weight of marketable fruit as VAM+ plants) for capsicum plants grown in the field trial over a range of relative yields. Relative yield was calculated as the fresh weight of marketable fruit expressed as a percentage of the maximum value of 35.5 t/ha. Values were determined from the Mitscherlich ($Y = a + be^{-kX}$) equations fitted to the VAM+ and VAM– means presented in Fig. 3*b*. P-equivalent values <64% relative yield were derived by extrapolation of the VAM+ curve presented in Fig. 3*b*, whereas values <20% relative yield were derived by extrapolation of both the VAM+ and VAM– curves presented in the same Figure. Dashed lines show that at 95% of maximum yield of fresh marketable fruit, 87.0 kg/ha more P was required by VAM– than by VAM+ plants.

VAM+ plants grown at all treatments except P_1 (Fig. 3*b*). Therefore, it is plausible that the gross margin values corresponding with these treatments also did not differ. Gross margins were negative for VAM– plants grown at P_1, P_2, and P_3 and for VAM+ plants at P_1.

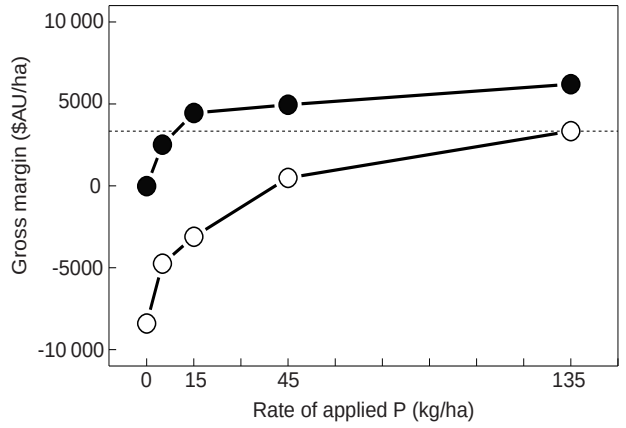

Fig. 6. Gross margin values calculated from the yield of fresh marketable fruit harvested from capsicum plants grown in the field trial. Plants were grown in the presence of a live (VAM+) mycorrhizal network (●) or a killed (VAM–) network (○). The gross margin which is maximal for VAM– plants ($AU3340) appears as a horizontal dashed line.

Discussion

Initial growth responses

Treatment P was applied as a narrow band to soil beds, and the transplanted seedlings would not have reached and benefited from this fertiliser until their roots had grown near the band. Similarly, any growth benefit from VAM colonisation would not have taken place until new roots had grown into the surrounding soil containing the network of mycorrhizal propagules. The greater ($P < 0.05$) leaf width at 21 DAT of VAM– plants grown at P_5 than at P_1 or VAM+ plants at P_1 (data not shown) suggests that the initial growth response to improved P nutrition originated from the band of superphosphate and not the mycorrhizae.

The greater ($P < 0.05$) P concentrations measured at 32 DAT in the YML of VAM+ than of VAM– plants grown at $\leq P_3$ (Fig. 1*a*) indicated that the mycorrhizal network had benefited the VAM+ plants. Colonisation of roots was also confirmed for VAM+ plants at 32 DAT (Table 3), although values were comparatively low. The greater plant heights measured at 35 DAT for VAM+ than for VAM– plants grown at P_1 are a direct result of the enhanced P nutrition of the mycorrhizal plants grown in the absence of fertiliser P.

Concentration of phosphorus in the index tissue

The importance of VAM in improving the early P nutrition of the capsicum crop grown in a low-P soil was established from this study since the P concentrations in the YML of VAM+ plants were greater than those in VAM– plants at low to moderate rates of P application ($\leq P_4$). This improved P nutrition associated with the mycorrhizae was also demonstrated by the achievement of adequate P concentrations in the YML for VAM+ plants grown at $\geq P_2$ and for VAM– plants at $\geq P_4$ only. The benefit of the VAM inoculum was obviated at P_5, at which similar index tissue P concentrations were observed in VAM+ and VAM– plants.

Factors influencing VAM parameters

Temporal changes in VAM colonisation

The temporal changes in VAM colonisation of the capsicum seedlings (Table 3) were consistent with a sigmoidal response. After planting the capsicum seedlings into the field, all roots localised within the plug of potting mix were initially non-mycorrhizal, and only new roots which grew into the surrounding soil would have become colonised; therefore, a high proportion of the total root length would not have been colonised until a significant amount of new roots had grown into the surrounding soil. This scenario may explain the fact that the development of the VAM symbiosis was relatively slow (e.g. back-transformed means for the colonisation percentage of VAM+ plants were only 2.9–6.3% at 32 DAT, Table 3). A large increase in the colonisation of roots of VAM+ plants from 32 to 43 DAT (Table 3) probably coincided with a rapid expansion of roots into the soil containing the intact network of mycorrhizal propagules.

Despite the initially slow colonisation of roots of VAM+ plants, the time from transplanting the non-mycorrhizal capsicum seedlings to maximal root colonisation (approximately 50 days, Table 3) was only slightly longer than the time from seed sowing to maximal colonisation reported for other crops in both the greenhouse (36 days for cowpea; Ikombo *et al*. 1991) and the field (48 days for corn; McGonigle and Miller 1993*b*).

Effect of phosphorus on VAM colonisation

Addition of P fertiliser with an associated increase in index tissue P concentrations did not diminish the mycorrhizal colonisation of roots of VAM+ plants. A possible explanation may relate to the high inoculum potential of the intact network of VAM propagules in the undisturbed soil prior to transplanting (1061 non-dormant infective propagules/g air-dry soil). The decrease with P application ($P < 0.05$) of mycorrhizal colonisation of roots (transformed scale) of VAM– plants at 149 DAT (Table 3) [associated with increased ($P<0.05$) P concentrations in the YML at earlier sampling times, Fig. 1] concurs with this explanation, since the initial inoculum potential of the fumigated soil was extremely low (theoretically 0). The importance of the mycelial network as a component of the inoculum potential of an undisturbed soil has been reported previously (e.g. Jasper *et al*. 1989; Evans and Miller 1990). Therefore, the widely held view that addition of P fertiliser (either in a band or broadcast) reduces VAM colonisation of roots may not always be correct, since the inoculum potential of the soil prior to application of P may over-ride the effect to some degree.

Relatively undiminished mycorrhizal colonisation of roots of VAM+ plants at high P rates may also be explained by the fact that the roots which were selected for the determination of colonisation percentage had grown within the entire volume of soil available in each bed, both within and outside of the narrow band of applied P. Owing to the relatively low volume of the P bands, even at the highest rate of application, the majority of roots probably grew outside these fertiliser zones. Therefore, despite the likely reduction in VAM colonisation of roots in the P band, overall values were high. This hypothesis is consistent with the finding of Lu *et al*. (1994) that arbuscular colonisation of corn roots growing outside the zone of P placement was greater than that of roots growing inside. The agronomic implication of this scenario is that although a fertiliser band may reduce VAM colonisation of roots in the band volume, the VAM symbiosis may be well developed outside this volume and be an important contributor to the P nutrition of the plant.

Although not appropriate in the present study, another reason for an absence of an effect of P addition on mycorrhizal colonisation of roots may be related to the adaptation of the VAM population to high P. However, the low level of P in the soil used in the present study (2–14 mg $NaHCO_3$-extractable P/kg) did not allow this hypothesis to be tested.

Fruit yield parameters

Mycorrhizae enhanced the P nutrition of plants grown at low P rates, as shown by the greater weight of marketable fruit produced by VAM+ than by VAM– plants at $\leq P_3$ (Fig. 3*b*). For each of the fresh fruit yield parameters, the lack of any difference between VAM+ and VAM– plants at P_5 was an indication that application of P_5 was sufficient to eliminate the P benefit gained from the VAM. Therefore, the general premise that the importance of VAM in agriculture is diminished when high rates of fertiliser (especially P) are applied concurs with the findings of the present study.

The proximity of a band of applied P to the seeds or seedlings planted within the bed may be a critical factor in determining the importance of VAM in later growth responses. Because the capsicum seedlings were planted directly above the narrow band of milled superphosphate in the present study, the initial growth response to improved P nutrition most likely originated from the band of P and not the mycorrhizae. However, in situations where P is applied as a band at a considerable distance to the side of the row of seeds or seedlings, a significant amount of time may elapse before root growth near this band or diffusion of P from the zone of fertiliser placement would benefit the P nutrition of the plant. This scenario would only apply in situations where the P band is $\geq$10 cm from the row of seeds or seedlings, since Moody *et al*. (1995) showed that the movement of P into the soil from a simulated band of $Ca(H_2PO_4)_2.H_2O$ plus $CaSO_4.2H_2O$ (superphosphate) was as great as 20–25 mm in 5 days in some soils.

P-equivalent

The progressive increase in the P-equivalent value with increasing relative yield (Fig. 5) reflected the fact that the VAM+ plants approached a yield plateau with the addition of much less P than did the VAM– plants (Fig. 3*b*). The results showed that a considerable saving in P fertiliser could be made by mycorrhizal compared with non-mycorrhizal plants, since the achievement of 95% of maximum yield of fresh marketable fruit required 87.0 kg/ha more P for VAM– than for VAM+ plants (Fig. 5).

The carbon drain hypothesis

The absence of reduced yields of VAM+ relative to VAM– plants grown at any P rate in the field trial was in contrast with the tendency towards a growth depression of mycorrhizal compared with non-mycorrhizal plants at ≥9.2 mg P/kg oven-dry soil in greenhouse experiments reported by Olsen *et al*. (1999). Whereas starch concentrations of roots of VAM+ and VAM– capsicum plants grown in the field did not differ in the present study, concentrations were lower for mycorrhizal than for non-mycorrhizal plants grown in the greenhouse experiments conducted by Olsen *et al*. (1999). These comparisons support the hypothesis that the responses

measured in the greenhouse may be attributed to insufficient production of photosynthate by VAM+ plants to meet the C demand of both host and endophyte. In the field trial, however, it can be concluded that production of photosynthate was surplus to the requirements of the plant and fungus, despite the fact that mycorrhizal root systems are estimated to require 1.5–20% more photosynthate than non-mycorrhizal roots (Jakobsen and Rosendahl 1990; Eissenstat *et al*. 1993; Pearson and Jakobsen 1993).

It was proposed by Olsen *et al*. (1999) that the C-drain by the mycorrhizae in the greenhouse experiments would have been exacerbated by low irradiance. However, although the mean irradiance during the production phase of the field trial (12.1 MJ/m^2.day) was greater than that estimated for one of the greenhouse experiments (8.4 MJ/m^2.day), it was similar to the mean irradiance measured during the production phase of the other experiment (13.4 MJ/m^2.day). Therefore, the low irradiance in the former greenhouse experiment probably exacerbated the C-drain of the fungus on the host plant, whereas, in the latter greenhouse experiment, it is plausible that some other factor(s) may have contributed to this effect. For example, the efficacy of the various VAM species, the edaphic properties such as soil moisture, the volume of soil available for root growth, and the soil and air temperatures differed between the greenhouse and field environments and may have contributed to the variation in response.

Type of VAM inoculum

Owing to the minimal disturbance of the soil in the preconditioning and production phases of the trial, it was likely that the VAM propagules belonged to most of the 5 major groups identified by Tommerup (1992): asexual spores, zygospores, hyphae in dead root-fragments, hyphae (±vesicles) in living roots, and extraradical hyphae. Previous studies have shown that the role of soil disturbance in reducing the P benefit to subsequent crops from an existing VAM association is quite invariable, irrespective of whether or not mycorrhizal colonisation is changed by disturbance (McGonigle and Miller 1993*a*). The mechanism for this effect is believed to be related to disruption of the extraradical mycelium (Miller *et al*. 1995), which, if undisturbed, may offer a seedling a linkage to an extensive system of hyphal pipelines ramifying into the surrounding soil (Evans and Miller 1990). It was likely that the extraradical mycelium developed in the preconditioning phase of the present study played an important role in the mycorrhizal response of the capsicum crop.

Economics

The importance of marketable yield as a determinant of profitability was one of the main reasons for the similar, or slightly higher, gross margins for VAM+ plants grown at all treatments (except P_1) and that for VAM– plants grown at P_5 (Fig. 6), at which the maximal yield was attained for VAM– plants. The weight of marketable fruit harvested from plants grown in these respective treatments did not differ at $P = 0.05$ (Fig. 3*b*). Therefore, the comparatively higher gross margins of VAM+ than those of VAM– plants grown at $\leq P_4$ reflected the greater ($P < 0.05$) weight of marketable fruit harvested from the former plants, rather than any savings in the cost of P fertiliser. The negative gross margins for VAM– plants grown at P_1, P_2, and P_3 and VAM+ plants grown at P_1 (Fig. 6) highlighted the increased profitability of VAM+ plants at low rates of applied P.

In an intensive horticultural crop such as capsicum, the cost of P fertiliser is a minor component of the total cost structure. For example, for a crop in which the soil is fumigated prior to planting and 135 kg P/ha is applied (such as VAM– plants grown at P_5), the total cost of all fertilisers with P (i.e. Q5 and superphosphate) is $AU697/ha. This amount represents only 6.6% of the total production costs and, assuming a yield of 4582 cartons/ha, only 2.1% of the total costs. Therefore, any decision to include VAM into the cropping system should not be based solely on the saving in cost of fertiliser P.

Provided soil-borne pathogens are not present at a yield-limiting level, some cost-saving can be achieved in the decision not to fumigate. The net saving of this decision is the cost of the fumigant ($1321/ha) less the cost of labour to remove emerging weeds from the plant-holes in the plastic mulch film if the fumigant was not applied ($529/ha). The cost of actually administering the fumigant to the soil is negligible, since the CH_3Br and CCl_3NO_2 mixture is applied whilst the plastic mulch film and trickle-tubing are being laid over the formed beds of soil. Again, however, this net saving ($792/ha) represents only a minor proportion of the total costs.

In an intensive horticultural system, most growers attempt to minimise the risk of low production as they are aware of the importance of marketable yield as a determinant of profitability. A typical risk-management strategy in the absence of decision-making tools (e.g. sap nitrate testing, bug checking) is to err on the side of caution when making the decision to apply relatively low-cost inputs such as fertilisers or pesticides. In the Bundaberg district, growers will often fumigate soil prior to planting tomato or capsicum crops if there is a chance of weeds or soil-borne pathogens limiting the yield potential of the crop. Herein lies one of the major limitations in the adoption of VAM in the standard cultural procedures of a crop such as capsicum. Application of superphosphate is an inexpensive and simple operation which gives consistent results. The reliability of VAM to enhance the P uptake of the crop may vary with length of fallow; previous cropping sequence; tillage practices; soil nutrient status; fertilisers, lime, and pesticides applied; and the VAM-dependence of the host crop planted (Thompson 1994). Other factors such as soil temperature (Borges and Chaney 1989) and light availability (Tinker *et al*. 1994) may also limit the effectiveness of the VAM symbiosis during crop growth.

The use of VAM in a cropping system offers more advantages than increased P nutrition to the host crop. For example, VAM have been associated with increased tolerance to water stress (Nelsen and Safir 1982) and decreased susceptibility to a variety of plant diseases (Linderman 1994); mycorrhizae have also been associated with improved soil structure by stabilisation of soil aggregates (Tisdall 1994). These benefits, however, are difficult to quantify, and therefore, it is likely that mycorrhizae will be perceived as little more than a substitute for P input; such a premise will limit adoption of VAM using current practices which are focussed on short-term gains. However, in the longer term, it is possible that VAM may become an integral component in sustainable production systems which have a lesser reliance on chemical inputs (particularly fumigants) and a greater focus on the diversity and health of beneficial soil organisms than conventional farming systems.

It is plausible, however, that future conditions may change the willingness of growers to adopt the use of mycorrhizae in intensively grown, VAM-dependent crops such as capsicum. For example, world reserves of phosphate are declining (Maronek *et al*. 1981), so the cost of P may dramatically increase in the future. It is also possible that environmental protection legislation may be introduced to limit P application rates to crops, as is the case for N fertilisers in some parts of Europe. For example, P, which can be transported into aquatic systems by sorption onto eroded colloidal particles, has been linked to eutrophication in 6 coastal and inland water bodies in southern Australia and may affect coral growth directly through an inhibition of calcification (Hunter 1992).

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