Effects of a Sugar-Factory Byproduct Compost on Root Growth and Mycorrhizal Infection of Sugarcane in Barbados

> (c) Peter F. Dunfield Department of Geography McGill University, Montreal March, 1991

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ABSTRACT

A compost consisting 95% of the sugar mill byproducts: bagasse, filter press mud, and fly ash, applied at 5 t ha^{-1} , increased vesicular-arbuscular mycorrhizal infection of sugarcane roots in one of three experimental fields in Barbados. In a plant cane field, compost stimulated formation of intracellular hyphal coils and arbuscules, but not vesicles or hyphae. Infection was greater in roots 35 cm and 65 cm than 5 cm distant from the plant stem, and compost effects were not significant at 5 cm. Two other sources of phosphorus, filter press mud and triple superphosphate, did not affect and suppressed mycorrhizal infection, respectively. Two ratoon crops showed no residual effect of compost on mycorrhizal infection. Compost also stimulated tillering, phosphorus content, and perhaps yield of cane, but did not differentially effect high versus low tillering or sloped versus flat areas. Root length, weight, and specific root length were unaffected by compost addition, but root branching was decreased.

RESUME

Un compost composé de bagasse, de cendre, et de boue de filtre d'une usine de sucre, appliqué à 5 t ha⁻¹ sur un champ de cane à sucre de première année à la Barbade, a stimulé l'infection des racines par des endomycorrhizes à vésicules et arbuscules. Le compost a stimulé la croissance d'arbuscules et d'hyphes enroulés intracellulaires seulment. Des vésicules et d'hyphes droites n'ont pas été affectés. L'infection était plus forte à des distances de 35 cm et 65 cm qu'à 5 cm des tiges des plantes, et la stimulation mycorrhizienne par le compost n'était pas significative à 5 cm. Deux autres sources de phosphate, la boue de filtre et le superphosphore triple, n'ont pas affecté et ont supprimé l'infection mycorrhizienne, respectivement. Deux champs <<ratoon>> n'ont pas exhibé des effets residuels de l'application Le compost a aussi stimulé le contenu en phosphore de compost. des feuilles, le nombre des tiges, peut-être la production de la cane, mais il n'y avait pas d'effets differentiels du compost sur les régions hétérogène du champ. La longeur et la pesanteur totale des racines n'ont pas été affectées par le compost, mais le nombre des ramifications a diminué.

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CHAPTER 1: Introduction and Literature Review

The tropical context

Improved understanding of environmental constraints peculiar to the tropics such as higher races of rainfall-induced leaching and runoff than in temperate areas (Ewel, 1986), concerns about "sustainability" of systems based on high inputs (Marten, 1988; Stinner and House, 1989), and economic constraints like the present cost of inorganic fertilizers, have led to a reevaluation farming technology in tropical agroecosystems. οŕ Sustainability, the maintenance of yield over time, is a complex property tied to social, ecological, and economic variables. It depends not only on environmental effects of an agronomic system, but also on how local credit systems buffer farmer debt load (Marten, 1988). Given the economic problems faced by much of the tropical world, locally-produced agricultural resources and technologies can be a vital contributor to sustained economic and ecological productivity. There is a need for small-scale, onfarm research programs geared towards site-specific problems (e.g. Sanchez and Benites, 1987).

Interest is growing in recycling of agricultural waste products for use as fertilizers and soil amendments. Sugar mills, for example, produce vast quantities of fly ash and filter press mud, substances of potential agronomic value (Hudson, 1989a, Prasad, 1976a). Over thirty thousand tonnes of filter mud are produced in Barbados each year. At an application rate of 25

t ha⁻¹, one half to one third of cultivated canelands could be amended with this substance annually (Walker, 1986). Composting these wastes is an alternative valuable in reducing bulk volume and producing a stable product (Crawford, 1983).

Field application of agricultural wastes has the dual value of returning nutrients removed with crops, and raising soil organic matter levels. Proponents of "sustainability" often stress the need for agricultural systems to mimic natural ecosystems (Sanchez and Benites, 1987). Minimizing system outputs, and retaining nutrients in organic residues rather than the inorganic soil pool, is the usual situation in natural tropical ecosystems.

Barbados sugarcane agriculture

The island of Barbados, situated at 13°10'N, 59°35'W, has a commercial agriculture based almost entirely on sugarcane. Soils are derived from parent limestone and depositional volcanic dust. They are slightly alkaline (pH averaging 7.6), with kandoid and smectoid clay contents above 50%, and commonly only 3-4% organic matter. Average annual rainfall is about 150 cm, varying from 108 cm at sea level to almost double that at the highest elevations, and is marked by a distinct dry season from December-January to June-July. Average temperature is 26°C, and temperatures rarely fluctuate below 19° or above 31° (Halliday, 1956; Hudson, 1970).

Sugarcane in Barbados is propagated from clonal stem

cuttings, at a planting density of one cutting per 46 cm, in rows 170 cm apart. Planting takes place in October to December, harvest from early January to late June. The first (plant) crop is generally given sixteen to eighteen months to mature, ratoon crops are then taken in each of the succeeding three years.

Since 1960, sugar production has declined dramatically in Barbados. A large proportion of the decline is traceable to acreage dropping out of cultivation, however there has been as much as a 30% decline in yield per hectare (Hudson, 1989b). Many factors may be responsible for this loss of productivity. A decline in organic matter, and related phosphate deficiency, may be a contributor in some areas, as evidenced by dramatic results from composting experiments (Hudson, 1989b). Leaf analyses have shown plant phosphorus contents to be marginally below levels considered optimal for growth (BSIL Agronomic Committee, 1986).

Recommended fertilizer application is 135 kg ha⁻¹ of compound NK (equal amounts) mix (de Boer, 1988a). Further additions of N have not significantly improved yields in most cases, indicating that inorganic nitrogen application rates are at an optimum (de Boer, 1989). There may be problems associated with leaching of nitrogen in heavy rainstorms, and other factors limiting plant fertilizer recovery, however these cannot be overcome merely by accelerating application rates.

The origin of the fertilization program can be traced back as far as the experiments of Saint (1932; reported in Humbert, 1968). He found N, K, and H_2O to be the factors most limiting

sugarcane growth on Barbados. Results of phosphorus applications have usually been inconclusive, perhaps because of the fixation capacity of clay soils. Saint (1932) believed there to be no need for phosphate fertilization because cane has a small requirement for this element, and available levels in soil were usually adequate. As well, phosphate removed with the crop was reapplied in the form of pen manure and filter press mud. Cane is also efficient at recovering phosphorus atlow soil availabilities (Humbert, 1968). Saint's program on fertilization and 'organic' farming - for example, mulching with sourgrass to conserve soil water and phosphate - contributed to appreciation of soil organic matter levels (Robinson, 1951).

In the forties, Sir Albert Howard took note of "...the case of the sugar industry in Barbados, where of recent years the replacement of organic manure by artificials has led to the virtual collapse of the island through disease and to a decision to re-introduce mixed farming...." (Howard, 1947). The mulching practices of Saint were abandoned in the 60's due to cost and fire risks, a loss which certainly contributes to the present decline (Hudson, 1989b).

The Agronomy Research Unit (ARU) of the Barbados Sugar Industry Limited (BSIL) has recently begun production and testing of a compost based on sugar factory byproducts (95% bagasse, filter press mud, fly ash; 5% chicken manure). The composition of the compost is outlined in Table 1. Consistent yield benefits averaging 2.2 to 8 t ha^{-1} , depending on fertilization, have been

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documented. Sugarcane has responded to fertilizer beyond the recommended dosage in the presence of compost (de Boer, 1989). Studies in Taiwan (Friedrichsen and Wei, 1969/1970) and South Africa (Moberly and Meyer, 1978) have shown dramatic yield benefits with similar factory-based composts. Whereas these yield benefits were insufficient to merit the cost of compost production, due in part to improved fertilizer response the BSIL compost is economically justified.

'Table 1: Chemical composition of compost used in strip plot trials, based on analyses of several samples in 1987-1988^A. Values presented are ranges, not averages.

Character	Level
pH in water percent moisture organic carbon organic matter total N P as P_2O_5 K as K_2O Ca Mg Na C/N Zn Cu Fe Mn	7.2-8.2 15-40% 18-30% dry matter 30-60% dry matter 1.0-1.7% dry matter 2.0-3.2% dry matter 0.6-0.8% dry matter 0.1-4.2% dry matter 0-0.4% dry matter 10-24 200-500 ppm 60-170 ppm 10000-30000 ppm

A Courtesy BSIL

Only 5 t ha⁻¹ of compost is applied. The majority of studies reviewed in Chapter 1 dealt with much greater additions, generally 20-50 t ha⁻¹. Dalzell et al. (1987) recommend compost additions of 25-30 t ha⁻¹, with an absolute minimum of 7.5 t.

Hypotheses

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The following study was undertaken to examine the effects of compost on root growth and mycorrhizal infection of sugarcane. The objective was to establish the potential for some biological factors other than simple fertilization to be contributing to yield benefits from compost application. Assuming phosphorus has become limiting to growth in some canefields, it is believed VAM is now a vital factor in crop nutrition. The hypotheses tested were:

a) Compost improves phosphorus nutrition of sugarcane.

b) Compost increases, or at least does not depress mycorrhizal infection of sugarcane. A removal of P limitation could partially explain crop response to heightened nitrogen additions. Compost itself is a phosphorus fertilizer, but should have differing effects on VAM than triple superphosphate.

c) The compost is most beneficial in low-yielding areas.

d) The organic matter complexes with the NK fertilizer and prevents its erosion during rain episodes.

e) Compost alters the root architecture of the cane such that a greater volume of soil is explored with less energy investment by the plant into root mass. SRL, total root length, and the number of higher order laterals should be decreased by compost, due either to greater nutrient availability or improved mycorrhizal status. If so, compost could contribute to more efficient water and P recovery from soils. Literature Review: Compost, soil organic matter, and plant nutrition

Organic matter is of fundamental importance to plant health, especially in the tropical world where soils are often poorly structured and impoverished of nutrients. Field application of composted organic wastes is an ancient practice in the tropics, a practice beneficial to the crop-plant system in diverse ways. Scientific interest in composts probably originated with Sir Albert Howard (1944), who developed the Indore process of composting organic wastes in India.

Howard was also interested in the association of vesiculararbuscular mycorrhizae (VAM) with plants. He saw this association as arising from good soil health (i.e. organic matter), and potentially vital to balanced plant nutrition. Much research has been generated in the past half century on the role of VAM in natural and agricultural systems, and the potential value of fostering or inoculating VAM in agricultural enterprises.

The remainder of Chapter 1 explores some interrelationships among compost (along with other sources of organic matter and nutrients), vesicular-arbuscular mycorrhizae, and plant health, particularly as they relate to the growth of root systems. References are taken from diverse ecological and geographical contexts, but where possible focus on the tropical world.

Compost-Soil Organic Matter

Composting is "... the decomposition or breakdown of organic waste materials by a mixed population of micro-organisms... in a warm, moist, aerated environment." (Dalzell et al., 1987) The process and techniques of composting are described by Crawford (1983) and Dalzell et al. (1987). The humic product has value as a fertilizer and soil conditioner.

Chemically, humus has a cation exchan e capacity, alters soil pH, and acts as a slow-release fertilizer (Godden et al., 1987). Organic fertilizers do not produce such a sudden, episodic flush of nutrients as do inorganic fertilizers, and may therefore be more fully utilized by plants. Because of its beneficial effects on soil chemical and physical properties, because microbes feeding on it immobilize nutrients against leaching, compost also can improve plant recovery of inorganic fertilizers when the two are applied together (Dalzell et al., 1987), although the opposite can also occur (Del Zan et al., 1987).

Physically, organic matter tends to damp out soil temperature fluctuations. It limits soil erosion by absorbing raindrop impact and stabilizing soil aggregates. Soil structural changes resulting from organic amendments (Paul, 1974; Salem et al., 1987; Mbagwu, 1989; Mbagwu and Piccolo, 1990) can lead to increased water holding capacity, increased hydraulic conductivity (Guidi and Poggio, 1987; Mbagwu, 1989) and lowered resistance to root penetration. Soil properties are directly

linked to pest populations, providing habitat for pests and their "enemies" (Hoitink et al., 1987).

Biologically, organic matter is a substrate for microbial growth, additions commonly inflating soil microbe counts (Adams and Laughlin, 1981; Pera et al., 1983; Godden et al., 1987; Novakova, 1987). Specific proliferation of nitrifying and cellulolytic bacteria (Rutili et al., 1987) and diazotrophs (Jodice and Nappi, 1987) has been noted. Different microbial populations have differing effects on plants. Some, for example, release phytohormones stimulating root growth (Ewel, 1986), while others influence nutrition directly.

The balance of diazotrophs, nitrifyers, and other bacteria important to the nitrogen cycle depends on the C/N ratio of the organic matter. Undecomposed trash is a good substrate for nitrogen-fixers (e.g. Patriquin, 1982), while substrates with low C/N ratios usually are not. Whether or not plants substantially benefit from the activity of free living diazotrophs is a matter of debate (Tinker, 1984).

Godden et al., (1987) found increased microbial enzyme activity in soil after 30 t ha⁻¹ of a cattle manure compost was added. The compost stimulated microbial phosphatase activity, while other factors causing microbial proliferation did not. Godden's compost was probably then a phosphorus source. Microbially induced solubilization of phosphorus through pH change or production of chelates and anions can increase the plant-available phosphorus pool, and certain microbes directly

alter phosphorus uptake properties of plant roots (Tinker, 1984). Any influence of organic matter on mycorrhizae, and consequent effects on phosphorus nutrition, are explored in a subsequent section.

Vesicular arbuscular mycorrhizae

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Vesicular-arbuscular mycorrhizae (VAM) is the general name of a group of aseptate fungal species of the family Endogonaceae which associate endotropically with the roots of many higher plants. The association is ubiquitous, and considered to be symbiotic. Exchange of carbohydrate (to the fungus) and nutrients (to the plant) has been unequivocably demonstrated (Cox et al., 1975).

The only nutrients known to be transferred directly to plants by VAM are P, Cu, and Zn, but inadequate phosphorus nutrition interferes with a plant's capacity to scavenge S and K (Harley and Smith, 1983). Primarily through these nutritional benefits, VAM infection commonly increases plant yield and reproductive character (e.g. seed weight: Khan, 1975). VAM is also implicated in altered plant disease resistance (Howard, 1947; Fitter, 1985b) and water relations. The latter may result from altered root architecture (e.g. Hetrick et al, 1988), reduced root resistance to flow (Harley and Smith, 1983), or decreased stomatal resistance mediated by VAM-produced hormones (Allen et al., 1980).

Ectomycorrhizae can utilize organic phosphorus sources, but in most cases VAM exploit only the labile soil pool (Tinker,

Suggestions that VAM recover plant-unavailable forms of 1975). phosphorus have arisen from experiments showing response of VAM plants, but not of non-VAM plants, to additions of rock phosphate (e.g. Daft and Nicholson, 1969), but this can be accounted for invoking VAM solubilization of rock phosphate. without Exploration of soil by mycorrhizal hyphae (Owusu-Bennoah and Wild, 1979), their proliferation around mineralization sites, and the greater K_m of hyphae than roots (i.e. recovery from lower solute concentrations) could explain it (Tinker, 1975; Harley and Smith, 1983). In support of this hypothesis, Pairunan et al. (1980) used a range of additions to show response curves of VAM and non-VAM plants to rock phosphate to be the same. VAM-plants simply had a vastly more efficient recovery.

Still, uptake of fixed phosphorus by potatoes has been suggested with radiographic techniques (in Gianazzi-Pearson and Gianazzi, 1983; Harley and Smith, 1983). There could conceivably be a relationship between VAM and phosphate solubilizing bacteria (Harley and Smith, 1983). Phosphorus solubility rises with declining pH, an effect potentially caused by VAM-respired CO_2 (Knight et al., 1989), or excreted H⁺ ions (Harley and Smith, 1983).

Most experiments demonstrating plant benefits from VAM infection have been laboratory-based. Demonstrations of benefit under natural field conditions, in non-sterilized soil already containing mycorrhizae, are scarce (Fitter, 1985b). The VAM association is symbiotic only under certain conditions easily

satisfied in a lab. VAM can be parasitic to plants grown on soil with abundant labile phosphorus (Khan, 1975; Smith, 1980), and to young plants not established well enough to accommodate a carbondrain (Fitter, 1985b; Dighton et al., 1987). Several studies have shown the association to be beneficial to plants grown in sterile soil only (St. John et al., 1983a; Hetrick et al., 1988; Kitt et al., 1988). In non-sterile-soil, VAM infection had no effect or was detrimental to plant growth, presumably because of microbial competition for P. A few studies have shown yield benefits from inoculation of non-sterile, field soil (Khan, 1975; reviewed in Plucknett and Smith, 1982).

Field benefits only accrue if the C/F ratio is high enough for the plant to accommodate the endophyte without itself becoming carbohydrate limited, and if phosphorus inflow is increased by the fungus. Merely because an endophyte transfers phosphorus does not prove it expands the phosphorus supply a plant could obtain on its own. Root longevity, nutrient uptake rates of uninfected roots, root extension rates, and soil water (as controlling phosphorus availability) control the balance between symbiosis and parasitism in the field (Fitter, 1985b).

Fertilizers and mycorrhizal infection

Inorganic phosphate fertilizer, usually as triple superphosphate, almost always depresses mycorrhizal infection of plant roots. Nitrogenous and compound fertilizers often have the same effect. A few examples of mycorrhizal suppression through inorganic

fertilization are outlined in Table 2:

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Element fertilized	Plant	VAM Index decreased	Reference
P	wheat, maize	* infection	Khan, 1975
p	wheat	* infection	Hayman 1975
P	subterranean clover	<pre>% infection, external hyphae, vesicles</pre>	Abbot et al., 1984
Р	tomato	<pre>% infection</pre>	Daft and Nicholson, 1966
Р	maize	<pre>% infection, chlamydospores</pre>	Daft and Nicholson, 1969
P	onion	<pre>% infection, arbuscules</pre>	Sanders and Tinker, 1973
Р	onion	<pre>% infection</pre>	Mosse, 1973
P	<u>Trifolium</u> <u>subterraneum</u> , <u>Erodium botrys</u> , <u>Lolium rigidum</u>	<pre>% infection</pre>	Abbott and Robson, 1979
P	Sudan grass	spores, arbuscules, external hyphae	Menge et al., 1978
P, PK	soybean, white bean	<pre>% infection</pre>	Buttery et al., 1988
NPK	rye	% infection	Strzemska, 1975
NPK	maize	spores	Kruckelmann, 1975
N	wheat	<pre>% infection</pre>	Hayman, 1975
N	<u>Pisum sativum</u>	<pre>% infection</pre>	Lanowska, 1966
N	winter wheat	spores	Hayman, 1970

Table 2: Experiments showing fertilization-induced decreases in indices of mycorrhizal infection.

The mycorrhizal endophyte appears to benefit plants in relatively infertile soils only. The usual hypothesis for the effect of inorganic phosphorus is that when root-obtainable quantities of phosphorus are sufficient for growth, the plant suppresses the association and its entailed carbohydrate drain.

While most studies of fertilization have been pot

experiments, there have been several field demonstrations of infection suppression with phosphate fertilizer. Khan (1974), for example, found 280 kg ha⁻¹ triple superphosphate to lower VAM infection of wheat and maize by up to 80%, although the effect was shown primarily on arbuscules and vesicles. "Parallel" hyphae ramified in the root cortex. Natural soil fertility can be used to predict infection intensity (Boerner, 1986; Kitt et al., 1988), and should influence the results of fertilization. Alleviation of severe phosphorus deficiency may not affect VAM infectivity whereas addition of luxury amounts undoubtedly will. Different soil types and VAM species can alter the dependency of infection level on nutrient levels (Bethlenfalvay et al., 1982).

The studies of nitrogenous fertilizers cited in Table 1 are simple pieces of a complex problem. While these often suppress VAM, and high leaf-nitrogen levels are usually correlated with low percent infection (Hayman, 1987), several experiments have shown opposing results (reviewed by Harley and Smith, 1983; Hayman, 1987). Pugh et al. (1981), and Mosse (1973) found that high nitrogen levels were necessary for maximum VAM infection of cotton and onion, respectively. Mosse believed mycorrhizal onions were prone to becoming nitrogen-limited because of their efficient phosphorus recovery. With added nitrogen, the suppression of infection by high soil phosphorus was removed. A large N/P ratio in the soil may therefore be necessary for a plant to obtain maximum benefit from the mycorrhizal association. Still, there are anomalies even to this generalization (Hayman,

1987).

Suppression of VAM by phosphate fertilizers may lead to Zn deficiency because of the vital role of the fungus in recovering this micronutrient (Singh et al., 1986).

Organic matter and VAM

It is well established that ectomycorrhizal development is stimulated by compost, peat, manure and humus (Slankis, 1974). Ericaceous mycorrhizae can assimilate organic nitrogen as amino acids directly from soils (Stribley and Read, 1980). Influences of organic compounds on the vesicular-arbuscular species is less well elucidated.

Laboratory studies of organic particles dispersed in sand show certain VAM species to possess limited saprophytic ability (Hepper and Warner, 1983; Dighton et al., 1987). Warner (1984) has proposed using peat as a carrier for VAM inoculant because the fungus invades organic fragments intracellularly and can survive periods of drying. VAM often survives on senescent roots, from there colonizing new root growth (Harley and Smith, 1983).

Microscopic studies with tropical trees (St. John et al., 1983a, 1983b) and sand dune grasses (Koske et al., 1975; Nicholson and Johnston, 1979), have found extraradical VAM hyphae, spores, and sporocarps associated preferentially with organic matter particles in sandy soil. Hyphae contact organic particles randomly, then proliferate in the same manner as roots in contact with rich microsites (St. John et al., 1983b). Although hyphae may associate with any mineralization site in the same manner (St John et al., 1983a), the potential value of organic matter in combination with VAM in poor (sandy) soils should, however, be underscored.

Several early agronomic mycorrhizal studies focused or. organic soil amendments. Sir Albert Howard's (1944, 1947) observations suggested positive influences of organic matter on the symbiosis. Earthing-up of cane in India, a process incorporating humus into the soil, stimulated soil proliferation of white mycelia Howard presumed to be mycorrhizal. In Louisiana sugar plantations humus addition stimulated VAM infection, while inorganic fertilizers either decreased it or prevented "digestion"- the arbuscular stage. In Indian tea plantations good levels of VAM infection were conditional on abundant humus. VAM was virtually absent from "poor and exhausted soils" (Howard, 1944).

Reed and Fremont (1935) reported better arbuscular development in citrus plants grown with farm yard manure (FYM) than with inorganic fertilizers. Positive influences of manure on total percent infection or arbuscular development were soon echoed in studies of strawberries, maize, and sea island cotton (reviewed by Mosse, 1963).

These studies may reflect the broad benefits of good soil health more than some direct stimulation of the mycorrhizal association by soil organic matter. As an example, pen manure

applied to sea island cotton stimulated total infection and the ratio of arbuscules to hyphae over both plants given an equal amount of NPK as inorganic fertilizers and plants with neither organic nor inorganic fertilizer. However, the organic addition used was 50% of total soil volume, and the soil used was a sand "low in organic matter and nitrogen and very deficient in available phosphorus and potash" (Johnston, 1949). The same extreme experimental design is true of Howard's studies: effects of only very substantial organic additions were noted.

Organic matter influences on soil properties are manifold, and where soil is severely lacking in good tilth and available nutrients, amelioration with organic matter can alter many properties which have a relay effect on mycorrhizae (see next section). The studies cited above do show organic additions to have stimulatory effects on VAM in extreme circumstances. Whether stimulation of the symbiosis is direct, or induced through improved soil health (structure, pH, etc.) is however, uncertain.

Boerner (1986) found VAM infection of forest herbs to be correlated to soil organic matter levels, but soil organic matter was correlated with other soil factors. High peat content of potting mix may actually inhibit VAM formation in certain horticultural plants, but this is likely to be a secondary influence of pH and can be counteracted by liming (Nemec, 1987). Organic matter, through its influence on soil fertility and structure, also affects the growth rate of plant roots,

especially fine roots (Mosse et al., 1981). As mentioned previously, percent infection is a function of root growth rates. Finally, organic matter has a phosphorus fixation capacity in certain (allophanic) soils, binding P through Al bridges (Borie and Zunino, 1983). Mycorrhizal infection is closely dependent on P-availability and, perhaps even more so, on the related measure of P-fixation capacity (Plenchette et Fardeau, 1988). Which particular properties of organic matter make it stimulatory (or inhibitory) to VAM formation is a matter of specific circumstance.

Recent agronomic studies are less consistent in their conclusions regarding manuring and VAM. Rutili et al. (1987) found depressed infection in soil ameliorated with composted cow manure, although this depression was less severe than with nutritionally equivalent amounts of inorganic fertilizer. In Poland, neither FYM nor inorganic fertilizer altered percent infection of wheat, while infection in rye was depressed by both, but only at high levels of the former (30 t ha⁻¹) (Strzemska, 1975). Manure may increase, decrease, or have no effect on different VAM spore populations in soils (Mosse and Bowen, 1968). Kruckelmann (1973) reported inorganic NPK and manure together to be stimulatory to VAM infection of maize; although addition of t ha⁻¹ year⁻¹ of manure for eighteen years did not 25 significantly affect soil spore counts (Kruckelmann, 1975). Ishac et al. (1986) found organic amendment to improve VAM status of maize.

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Addition of a poplar bark compost to vineyards increased VAM spore counts but not percent infection (Jodice and Nappi, 1987). There was, however, a proliferation of roots in the compost layer, and increased root growth rates could have diminished percent infection while increasing total infected root length. Application of a lignocellulose compost to an apple orchard led to higher spore counts and increased numbers of strongly mycorrhizal absorbing rootlets- again, primarily in the compost layer. The authors did not alter inorganic fertilization in these experiments, and the amount of compost used may have been sufficient to be considered a mulch, inducing secondary effects on soil temperature and water retention.

Obviously, the influence of particular organic sources will depend on their nutrient compositions. As already noted, the effect of inorganic nutrient additions is usually negative, but can become complex depending on natural soil fertility and N/P ratios. Kruckelmann (1975) found VAM spore counts to be differentially affected by manure addition, depending on soil type. Inconsistent results of recent experiments on manure additions may well be a result of a less extreme experimental design than that of the initial studies. Organic matter applied to a rich soil may add nutrients to suppress the VAM association, without substantially affecting soil structure or chemical properties. The degree of humification of the organic addition may also be a controlling factor (Rutili et al., 1987).

As a general conclusion, organic fertilizers have a less

inhibitory effect than do inorganics, and in certain cases even stimulate VAM infection over control, no-addition treatments. Where this is not due to a secondary effect on soil properties, it is probably tied to nutrient availability. Organic fertilizers are mineralized slowly whereas most inorganic fertilizers are immediately available upon application. The retention of nutrients in unavailable forms within organic complexes may prevent the triggering of whatever mechanism suppresses mycorrhizal association in the presence of high available nutrient levels. As well, hyphae will proliferate around mineralization sites, organic particles included, probably leading to an increasingly active, arbuscular infection. Evidence for a unique, direct association of organic matter and VAM is scant.

Other factors influencing VAM infection

Almost any soil factor can correlate with VAM infection, because a specific set of soil factors is interdependent. Day et al., (1987) traced differences in mycorrhizal infection of the same plant species along a toposequence. They attributed differences to soil texture changes, although P-availability, pH, and organic-carbon content also differed along the slope.

Soil moisture, pH, reactivity, cation exchange capacity and P-fixation capacity (to name a few) all influence ion mobility and availability, and therefore VAM infection (Janos, 1987). Soil factors will also directly influence the survival and

infective ability of VAM. Different soil types therefore often have different dominant mycorrhizal species (Bethlenfalvay et al., 1982). The effects of soil factors on VAM are reviewed by Harley and Smith (1983)

VAM infection, and the relative proportions of arbuscules, vesicles and hyphae, can follow seasonal cycles (Douds and Chaney, 1986). Most species have an optimal temperature of about 30° C (Harley and Smith, 1983). Light intensity controls plant photosynthesis, and thus also the supply of carbohydrate to the fungal symbiont (Harley and Smith, 1983). Dense root growth leads to more opportunities for infection points to occur (e.g. Warner and Mosse, 1982).

VAM, fertilizer, and root growth

Due to their vital role in plant nutrition, the growth of roots is intimately tied to soil fertility and VAM. Organic matter affects root growth and distribution (e.g. Howard, 1947; St. John et al., 1983b; Jodice and Nappi, 1987) through its influence on soil fertility, soil structure, and soil fauna, as noted earlier.

In natural systems, the energy plants expend on root growth is directly proportional to their degree of nutrient-limitation (Chapin, 1980). In nutrient-limited conditions, a large root mass is necessary to reach adequate reserves for optimal growth. Soil status of all major plant nutrients (and water) controls root growth, but phosphorus may be especially important. Because of its limited mobility, phosphorus depletion zones develop and

the plant must constantly reach new reserves.

Severe phosphorus deficiency reduce length and can initiation of lateral roots in grasses (Hackett, 1968; Christie, 1975; Drew and Saker, 1978). This is probably not an adaptive response, but a simple limitation of growth by malnutrition. Anderson et al. (1987) found root length to be increased by phosphorus additions. VAM infection was not depressed by the addition, again suggesting a situation where phosphorus was limited. May et al. (1965), using phosphorus levels above deficiency, found increasing total root length with decreasing P supply, a result more in agreement with the general rooting principle stated above.

Inadequate soil phosphorus may cause plants to develop high specific root length (SRL = length/weight) (Anghinoni and Barber, 1980; Fitter, 1985a; Hetrick et al., 1988). Large SRL values result from small root diameters and high proportions of fine laterals in a root system. This is an appropriate adaptive response to low ambient soil fertility, since phosphorus uptake per unit weight is inversely related to root diameter (Lewis and Quirk, 1967).

However, root systems respond to soil heterogeneity in a contradictory fashion, ramifying laterals into isolated nutrientrich pockets (Drew and Saker, 1978; Anghinoni and Barber, 1980; St. John et al., 1983a, 1983b). Phosphorus-enriched zones may therefore support localized relative increases in length and even SRL within root systems.

Another complicating factor is VAM. VAM are directly affected by phosphorus supply, and in turn affect root architecture. Root systems of VAM and non-VAM plants may therefore respond differently to soil phosphate supply.

VAM infection has been shown to increase the total root length of big bluestem (Hetrick et al., 1988), to increase root weight of yellow poplar and gum (Simmons and Pope, 1987) while having inconsistent effects on root length of the same species (Simmons and Pope, 1987, 1988), and to decrease SRL of cotton (Price et al., 1989). These effects may be primarily nutritional. VAM serve as a buffer against differential soils to supply phosphorus, through capacities of the preferential infection of plants growing in low-phosphorus conditions. In so doing, they may damp out the effects of phosphate on root growth. However, Price et al., (1989) found VAM plants to have fewer high order laterals than non-VAM plants, an effect also caused by P deficiency.

VAM have been implicated in the production of phytohormones (Allen et al., 1980) and may directly influence architecture. Because of a vastly more efficient exploration of soil by roots with hyphae than by roots alone, it may be advantageous for VAM plants to produce fewer high-order laterals and grow in a "herringbone" structure. The total soil volume explored by a "herringbone" pattern is greater than by a densely branched system of the same mass (Fitter, 1987). Fitter (1987) has pioneered the use of topological analysis necessary for

recognition of these differences. Although he predicted topology to be important primarily for mobile ions, the role of VAM hyphae in exploring soil and transporting phosphorus to the root surface may, functionally, make phosphorus a mobile ion. Hetrick et al., (1988) showed that, while VAM and P had many similar effects on root systems of big bluestem, only VAM affected topological character. Phosphorus changed topology solely through its effect on VAM.

Plant species particularly dependent on VAM for growth, like the Mangoliales, have certain common root characteristics: they are coarsely branched, large in diameter, and often lack root hairs (which are functionally the same as VAM) (Baylis, 1975; St. John, 1980). Although it is a cross-species comparison, Baylis' theorem lends credence to some of the VAM effects postulated in this section.

There are features of root architecture not accounted for by topology or common measures like SRL. These include link length (the distance between branchings or between a branching and terminus), and angle of branching (Fitter, 1987). These could conceivably also be altered by VAM.

<u>Conclusion</u>

A complex of factors comes into play when considering an ecological system even as simple as an agricultural operation. It is a futile task to isolate the effects of a compost in any particular context. It is a substance with inherent chemical

properties as divergent as the soil-environmental systems it is used on. The many direct and indirect effects of compost application may not all operate in the same situation, but many will.

The same argument is true of VAM-soil-plant connections. The importance of site-specific, field oriented studies is underscored by these heterogeneous effects.

However, both soil organic matter and VAM can be important indices of good plant health. The relationship between the two, and manipulation of each in the design of more efficient agricultural systems, deserves further study. The aim of this thesis is to do this in the Barbadian context.

CHAPTER 2: Experimental design and methodology

Experimental Design

During the 1989-1990 cropping season, observations were made on "strip plot" trials designed by BSIL'S Agronomy Research Unit. With this technique, field-long "strips" consisting of several plant rows receive experimental treatments using standard farm equipment. Strip yields (per metre row) are acquired during commercial harvesting simply by measuring the length of cane rows loaded onto carts which are routinely weighed at the sugar factory. The value of the strip plot technique lies in obtaining large sample harvests by standard farm methods (de Boer, 1986).

Effects of a sugar-mill byproduct compost (Table 1) were examined on experimental fields at three plantations in Barbados: Edgecumbe, Windsor, and Todds. Edgecumbe and Windsor are located in the Lowlands, and have Grey-Brown Association soils of predominantly smectoid clays overlying coral limestone. Todds is located in the Upland plateau, and has Red-Brown Association soils of kandoid clays overlying coral (Vernon and Carroll, 1965, using U.S.D.A classification standards).

Compost was banded (30 cm width) at 5 t ha⁻¹ onto plant cane only. The equipment used is described in Hudson and Bailey (1986). Standard NK fertilizer addition is 135 kg N ha⁻¹, usually of 22-0-22, banded (15 cm width) onto plant and ratoon crops.

At Windsor, compost was applied 15/04/87 to two twelve-row

strips, alternated with control strips. Samples were taken from the second ratoon crop.

The Todds experiment combined eight, six-row strips accounting for all combinations of three binary variables: inorganic 24-0-18 fertilizer (120 kg N ha⁻¹ vs. 150 kg N ha⁻¹ on plant cane and 133 kg N ha⁻¹ vs. 193 kg N ha⁻¹ on ratoon), compost (present or absent) and cultivar (62163 and 80689). Compost was applied on October 22, 1986. Sampling therefore involved the second ratoon crop. The Todds and Windsor fields were chosen from several ARU experiments because of positive response of previous crops to compost additions.

Edgecumbe contained three strips each of compost, filter mud $(25 \text{ t } ha^{-1})$, and control (no addition). The arrangement and dimensions of the strips are outlined in Figure 1. Triple superphosphate (TSP) was banded at 310 kg ha⁻¹ onto one strip of each treatment. This rate equates to 63 kg P ha⁻¹, somewhat more than an elemental P application rate of between 35 and 55 kg ha⁻¹ from compost (Table 2, using a moisture content of 27%). Application rates were recommended optima based on previous ARU experiments. Field applications were done on 05/05/88, after the field had been strip-tilled (de Boer and Hudson, 1987) rather than plowed conventionally.

Samples (for all measures except yield) were taken crosssectionally across strips, and each such transect considered a "block" (Figure 1). Except where otherwise noted, block positions were chosen using random number tables standardized to Figure 1: Outline of the experimental field at Edgecumbe, indicating relative outlay of strips, blocks, and plots.



field length. Portions of strips within blocks are referred to as plots (Figure 1).

This is not strictly a randomized block design since the arrangement of treatment plots within blocks is constant. This constancy was considered unlikely to lead to serious concomitance of treatment and environmental factors for two reasons. First, since cane rows were aligned with land contours, most microgeographical variation occurred within rather than across strips. Second, the presence of several treatment plots within each block should have reduced the influence of any environmental gradient. Still, effects of TSP at Edgecumbe are noted with special caution since all three plots were located at the south end of the field (Figure 1). At Todds, comparison of cultivars may be suspect for the same reason, but this was secondary to the main purpose of the experiment in any case.

Blocking was deemed practical for reducing background variation because of the distances covered by strips (typically 200 m or more), and gradations of crop growth along them.

Yield and Agronomy

Tillers per plant were counted at Todds on 21/09/89 (four blocks, ten plants per plot), and at Windsor on 10/10/89 (five blocks, ten plants per plot). Only visible cane stalks at 1 m height were counted.

In late October to November, 1989, counts were made of tillers per plant (ten plants per plot X ten randomly chosen

blocks), total numbers of tillers per 10 m row (nine blocks), and stalk circumference at 1 m height (21 stalks per plot X three blocks) at Edgecumbe. The field was harvested by hand March 9-15, 1990.

The number and species of weeds, the number of plants supporting climbing vines (primarily <u>Rhynchosia phaseoloides</u>), and the total length of ground covered with sourgrass (<u>Andropogon</u> spp.) at Edgecumbe, were counted for a single, entire interrow of each strip on October 4 and 8, 1989. The east and west sides of the field, as separated by an access road, were considered separately for these observations, being of roughly the same length (180 m). Gooding et al. (1965) was used as a guide to species identification.

Root morphology (Edgecumbe)

On October 18-26, 1989 a preliminary survey of rooting density was carried out. Four blocks were chosen: two on a dry plateau area and one on each side of a drainage ditch running roughly perpendicular to the cane rows. A soil core was taken 46 cm to the south side of a plant stem in each plot, using a 12.8 cm diameter auger driven to 19 cm depth.

Cores were stored at 20^oC for up to 10 days. Volume (by displacement) and weight were recorded. Because of the cemented nature of the clay, they were soaked in water for 48 hours to unconsolidate them before wet sieving roots with a 0.707 mm sieve. Sieve-recovered roots were blotted on paper towel,

divested of any visible mud, rocks and non-root plant material, weighed, and stored at $1^{\circ}C$.

Two-gram root subsamples were cut into fragments no longer than 3 cm and used for length estimation by the line intersect method (Tennant, 1975) on a 3 cm X 3 cm grid under a glass cover. Samples were oven dried at 55° C for at least 48 hours beforehand to aid handling and random distribution on the grid.

On February 3-6, 1990, a more extensive core sampling was carried out. This second sampling phase was intended to examine rooting parameters at several distances from the plant stems, and to accelerate sample processing. The earlier sampling may have allowed fungal proliferation in excised roots because of delays between coring and freezing roots.

An auger 6 cm in diameter and 21 cm in depth was used to take cores 8, 33, and 63 cm from the stem of one plant per plot in five blocks. The same blocks were used, with a fourth added to the midslope between the plateau and the drainage ditch and a fifth on a flat area. Cores were frozen immediately after sampling to preserve roots and aid in slaking away of clay blocks when soaked in water.

A 30 g soil subsample was taken from each core. These were pooled for each set of three cores per plant, ground through a 2 mm sieve, and saved for later analyses.

Frozen cores were soaked one hour, then transferred to a bucket equipped with an overflow spout. The spout was positioned over a 0.707 mm sieve to collect floating matter (i.e. roots).
Water at a constant flow rate was circulated into the bottom of the bucket for ten minutes, the settled soil agitated occasionally by hand.

Mealybug capsules collected in the sieve were counted and removed from each sample. Roots were separated from other materials, blotted on paper towel, weighed, and stored at 1^oC.

Roughly 0.3 g subsamples (less if obligated by sample size) were cut into fragments not longer than 3 cm and used for length estimation on a 2 cm X 2 cm grid (Tennant, 1975). The grid was also used as a guide in counting the total number of root branching points. Due to a paucity of roots in certain samples, they often needed to be saved for mycorrhizal staining after length estimation, and were therefore not oven dried.

Vesicular-arbuscular_mycorrhizae

Root samples from Windsor and Todds were taken within two weeks of harvest. For each plot of three blocks at Windsor, nine plants were pooled into a single sample. At Todds, six plants were pooled per plot at four blocks. Roots were excavated to about 5 cm depth using a trowel, at 5-15 cm and 25-40 cm from the cane stalks. An attempt was made to take similar amounts of root material from each plant (two 10 cm lengths of axes with attached laterals). Roots were washed and frozen immediately after sampling.

Root subsamples (2 g) from Edgecumbe, Windsor, and Todds were taken by cutting a 1-2 cm wide section from the frozen

samples. These were stored in FAA fixative (Phillips and Hayman, 1970) until stained.

Mycorrhizal structures were stained using chlorazol black E and the method of Brundrett et al. (1984), with the following modifications: the concentration of chlorazol black E in the stain solution was increased to 0.15%, the clearing period in KOH was 20 minutes and the staining time 2.5 hours at 90°C. Because of the dark pigmentation of roots, a decolorizing phase was added as in the method of Phillips and Hayman (1970). This involved bathing roots in 3% commercial hydrogen peroxide until colorless (generally 3 hours) immediately after clearing in KOH.

Percentage infection of 1989 samples was assessed using the gridline intersect method (Giovannetti and Mosse, 1980), at 50X magnification. One hundred intersections per sample were counted. Two distinct morphologies of endotropic fungi were counted: diffuse black areas seen by closer examination to consist of coiled hyphae and arbuscules (although these could 1*0t be distinguished with the dissecting scope), and thicker hyphae running transverse with the root and often bearing vesicles.

Infection of 1990 samples was assessed using the magnified intersections method of McGonigle et al. (1990). Roots larger than 2 mm in diameter could not adequately be flattened under a coverslip and were ignored. One hundred to 125 viewing passes were made at 4 mm distances along roots, occasionally fewer if total root length was inadequate, as in certain 65 cm cores.

The latter method was preferred since fungal morphology was

more apparent. Only hyphae seen to exhibit mycorrhizal character (aseptate with evaginations) were counted. Vesicles, intracellular coils, and arbuscules could all be distinguished, although in the typical infection unit arbuscule development was confined to the inner cortex. Coils and arbuscules commonly occurred together, and it was often difficult to distinguish amorphous, semi-degraded hyphal coils from arbuscules. Both, however, are considered signs of active infection.

Arbuscular, vesicular and hyphal (total) colonization (AC, VC, and HC, respectively) were calculated for each sample (McGonigle et al., 1990). The percentage colonization by hyphal coils (CC), arbuscules/coils (ACC-the percentage occurrence of coils, arbuscules, or both together), and transverse (intercellular) hyphae alone (THI) were calculated using the same principle. Also, infected root length (IRL= HC*total root length) and arbuscule/coil infected root length (ACRL= ACC*total root length) were calculated.

Soil tests

Edgecumbe soil samples were analyzed for loss on ignition $(420^{\circ}C, 45 \text{ min})$, and NaHCO₃-extractable phosphorus as described in McKeague (1978). The only procedural change was using Whatman 41 paper for filtering the P-extracting solution.

Mapping

The vertical geographical profile of the Edgecumbe field was

estimated at 10 m intervals using surveying stakes connected by a 6 m line bearing a level.

Leaf analysis

During harvesting of Edgecumbe, the youngest two fully-opened leaves of six plants per plot (pooled) in three blocks were saved, dried 48 hours at 95°C, chopped into 1-3 cm pieces to homogenize samples, and analyzed for total P using atomic absorption spectrophotometry.

<u>Data Analysis</u>

Analyses of variance (ANOVA) were calculated using Systat 4.01. ANOVAs for tillers per plant and mean stalk area were nested by plants within blocks. Normality was tested by the Komogorov-Smirnov test, and homogeneity of variance assured with residual plots. Square root and natural log transformations were needed in some cases to correct for violation of these assumptions.

To reduce the total, study-wide possibility of Type I error, related measurements on single sampling phases were analyzed using multivariate analyses of variance (MANOVA). Separate MANOVAs were:

1) Soil properties: loss on ignition * $(^1)$, air-dry moisture content, and available-P g⁻¹ soil (natural log transformed). Treatment, TSP, block, and treatment X block were the factors.

¹ Variables square root transformed for ANOVA are indicated by a superscripted asterisk (*).

Other interactions were ignored since TSP is immobile and should not theoretically show compound effects with slope or compost.

2) 1989 Edgecumbe roots: root length cm^{-3} soil *, root weight cm^{-3} soil *, SRL, HC, ACC, THC, IRL *, and ACRL *. Factors were treatment, block, and TSP, with no TSP X block or three-way interaction.

3) 1990 Edgecumbe roots: branches cm⁻¹ root, root weight *, root length *, mealybug capsules *, SRL *, standardized root weight * (the percentage in one core of the total root weight contained in three cores per plant), standardized root length *, CC, AC, VC *, THC *, ACC *, HC *, ACRL *, and IRL *. Factors were treatment, block, TSP, and core, with no three-way or fourway interaction.

4) Windsor mycorrhizal samples: VC *, THC, ACC, and AC. Factors were treatment, block, and core, with no three-way interaction.

5) Todds mycorrhizal samples: VC *, THC, CC, AC, ACC, and HC. Factors were cultivar, treatment, block, fertilizer, and core, with no three-way or four-way interaction.

In the event of a significant multivariate statistic, univariate ANOVAs were considered for each dependent variable in accordance with the Hummel-Sligo procedure (Barker and Barker, 1984). Factors at Todds and Windsor were binary and did not require multiple comparisons. Multiple comparisons for Edgecumbe were done using the Bonferroni technique.

CHAPTER 3: Results

<u>Yield</u>

Analysis of yield at Edgecumbe was made difficult by the loss of a control strip during harvesting. While treatment differences were not statistically significant, compost strips had the highest average yield and control strips the lowest (Table 3). TSP may have improved the yield in strips without compost addition. Compost application commonly results in comparable yield stimulation of 2-8 t ha⁻¹ (de Boer, 1989), and the large size of strips (the smallest are 1.8 ha) suggest these yields to be accurate. Harvests in the next three years should clarify compost effectiveness in this particular field.

Table 3: Yield^A of sugarcane in compost, filter mud, and control strip plots at Edgecumbe in 1990.

Strip	Treatment	TSP	Yield (t ha ⁻¹)
1	Control	No	92.2
2	Compost	No	102
3	Filter mud	No	98.8
4	Control	No	-
5	Compost	No	108
6	Filter mud	No	-
7	Filter mud	Yes	107
8	Compost	Yes	103
9	Control	Yes	102

A: Courtesy BSIL

At Windsor, where ratoon year is an additional factor, there has been a significant improvement of yield with compost addition (Two-way ANOVA; p=0.049)² (Table 4). No significant effects of fertilizer level or compost addition were evident at Todds (Fourway ANOVA) (Table 4).

Table 4: Yield^A of sugarcane in the Windsor and Todds experiments. Fertilizer levels are: 1=standard fertilization, 2=excess fertilization (see text). Cultivars are: 1= 62163, 2= 80689.

Field	Year	Fertilizer level/ Cultivar	Yield	(t ha ⁻¹)
			Compost	No compost
Windsor	1988	-	69.6	59.2
	1989	-	79.8	72.4
	1990	-	86.6	70.2
	Average	-	78.7*	67.2*
Todds	1988	1/1	112	108
		1/2	128	119
		2/1	112	108
		2/2	123	126
	1989	1/1	84.0	89.4
		1/2	82.8	80.6
		2/1	96.9	89.9
		2/2	82.5	68.4
	1990	1/1	86.2	75.9
		1/2	95.9	97.1
		2/1	86.7	89.5
	_	2/2	84.0	98.1
	Average	1/1	94.1	91.1
		1/2	102	98.9
		2/1	98.5	95.8
		2/2	96.5	97.5

A: Courtesy BSIL

Non-

*: Significantly different at p=0.05 level

² Except where otherwise noted, probabilities are calculated from ANOVA F-statistics, or in the case of comparisons among factor levels, are Bonferroni contrasts.

Agronomy

Compost addition had no significant effect on tillering of plants at Windsor (Two-way ANOVA) or Todds (Four-way ANOVA) (Table 5)³. There were significant block (p=0.001) cultivar (p=0.015) and block X cultivar (p=0.046) effects at Todds.

Both compost and filter mud significantly increased tillering per plant (Three-way ANOVA, p<0.01 in each case) and tillering per metre row (Three-way ANOVA, p<0.01 in each case) over control plots at Edgecumbe (Table 5, Figure 2). Filter mud had a greater stimulatory effect on per-plant tillering than did compost (p=0.018).

There were no significant triple superphosphate or treatment X TSP effects on tillering per metre row. However, considered separately, control plots with TSP did not have significantly fewer tillers per metre row than compost or filter mud plots without TSP (p=0.24 and p=0.19 respectively) (Figure 2). TSP addition reduced tillering per plant (p=0.030). Figure 2 shows this to be primarily due to reduction in filter mud plots, although the trend is not supported by a significant treatment X TSP interaction (p=0.10).

³ Standard errors (SE's) presented in tables and figures are pooled values, except in the case of variables transformed for ANOVA's. Where an inverse transformation has been done, actual SE's of factor-level (i.e. treatment) means are given. Where a square root transformation has been performed, presented averages are not true means, but squared mean-roots. Standard errors of these squared mean-roots have been calculated from pooled SE's separately for each factor-level mean. While the latter values are not strictly correct, they best illustrate statistical relationships among factor levels.

Figure 2: Stem growth parameters, +/- 1 standard error, of sugarcane plants under three experimental treatments at Edgecumbe. Hatched boxes represent plots with TSP added, open boxes plots without TSP.



There were no significant effects of treatment, block or TSP on mean cross-sectional stem area at Edgecumbe (Three-way ANOVA) (Figure 2, Table 5).

Table 5: Features of tillering: tillers per plant, tillers per m row, and stem cross sectional area, for compost and control treatments at each of the three experiments. The code for Todds plots is the same as in table 4 (fertilizer level/cultivar).

Experiment and featur	: N e		Pooled SE					
		compost	control	filter mud				
Windsor (tillers per plant)								
overall	100	10.69 A	10.27 Å	-	0.658			
Todds (til	lers per	plant)						
1/1	50	13.48	13.24		0.706			
1/2	50	13.46	11.40	-	0.706			
2/1	50	14.50	14.16	-	0.706			
2/2	50	12.38	12.74	-	0.706			
overall	200	13.46 ^A	12.89 A	-	0.353			
Edgecumbe	(tillers	per plant)						
+ TSP	50	5.82	4.86	7.06	0.359			
- TSP	100	5.79	5.15	5.84	0.253			
overall	150	5.80 ^B	5.05 A	6.48 ^C	0.114			
Edgecumbe	(tillers	per m row)						
+ TSP	18	7.33	7.12	7.58	0.150			
- TSP	36	7.34	6.73	7.55	0.106			
overall	54	7.34 ^B	6.86 A	7.56 ^B	0.0876			
Edgecumbe	(stem are	a in cm ³)						
+ TSP	63	6.29	6.72	6.37	0.339			
- TSP	126	6.38 _	6.69	6.49	0.239			
overall	189	6.35 ^A	6.70 A	6.43 ^A	0.196			

Different letters indicate significant "overall" differences in treatment means, at p=0.05 level. Note that N for the filter mud treatment at Edgecumbe is only 2/3 of given N values, and SE values for this treatment are therefore somewhat larger.

There were no significant treatment or TSP effects on any measures of weediness at Edgecumbe: species richness, number of cane plants supporting <u>Rhynchosia</u> or other climbing vines, or ground area covered by <u>Andropogon</u> spp. (Three-way, four variable MANOVA; Pillai trace p=0.27) (Table 6).

Table 6: Measures of weediness in Edgecumbe plots.

Measure	Compost (N=6)	Control (N=6)	Filter mud (N=4)	Pooled SE ^A
Species richness ^B	5.00	6.33	6.75	-
Number of <u>Rhynchosia</u> phaseoloides ^C	7.33	12.3	2.00	3.21
Total number of vine	es ^C 7.83	13.0	2.50	3.40
m ground covered by <u>Andropogon</u> sp. ^C	1.81	3.88	2.49	1.39

A: for N=6

B: Data were inverse transformed for MANOVA. Actual SE's are 0.37, 0.33, and 1.80 respectively for compost, control, and filter mud. C: per 180 m interrow

Leaf analysis (Edgecumbe)

Average elemental leaf phosphorus concentrations were: control= 0.118%, compost= 0.132%, filter mud= 0.132% (Figure 3). A threeway ANOVA revealed a marginally non-significant effect of treatment (p=0.058), with no block or TSP effects. Pooled, compost and filter mud treatments significantly elevated A 2.5 1

Figure 3: Leaf phosphorus content, +/- 1 standard error, for the three experimental treatments at Edgecumbe. Hatched boxes represent plots with TSP added, open boxes plots without TSP.

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Treatment

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phosphorus content over control plants (p=0.021)⁴.

Root morphology and vesicular-arbuscular mycorrhizae (Edgecumbe) 1989 Samples: Treatments and blocks did not significantly affect rooting or mycorrhizal infection in the preliminary samples. Only TSP resulted in a significant multivariate test statistic (Table 7). Examination of univariate ANOVA's was therefore merited for this factor only (Table 7).

Table 7: Multivariate and significant univariate F-statistic probability values from variance analysis of rooting parameters and mycorrhizal infection in 1989 Edgecumbe samples.

Factor		Variable								
	Root length	Root 1 weigh	SRL t	ACC	THC	НС	ACRL	trace)		
Treatment (Compost)	-	-	-	-	-	-	-	.767		
TSP	.003	-	.002	.009	-	.002	-	.026		
Block	.014	.012	-	-	-	-	-	.654		
Treatment X TSP	.040	-	-	-	-	-	-	.476		
Treatment X Block	-	-	-	-	-	-	-	.631		

⁴ Only two <u>a priori</u> contrasts were made here, due to the small sample size: (1) Compost plus filter mud versus control, and (2) Compost versus control plus filter mud. With Bonferroni methods, the hypothesis rejection limit is then 0.05/2=0.025. In all other instances, each treatment was contrasted singularly, the rejection value therefore being 0.05/3=0.017.

Total and arbuscule/coil colonization were both, as expected, decreased by TSP addition (Figure 4). SRL was increased by inorganic phosphate, due more to a (significant) increase in root length than a decrease in weight (Figure 4).

The causal connection between infection and SRL hypothesized in Chapter 1 seems unlikely to be operative here. The residual correlation coefficient between the two on a per-plant basis is weak (0.143 for SRL and ACC; -0.0407 for SRL and HC). While a high correlation would not prove causality, given that experimental treatments have a wide range of interconnected environmental effects, a low correlation certainly makes it unlikely. As well, the treatment in which SRL was most affected by TSP addition (filter mud), was the one in which infection was least affected.

<u>1990 Samples</u>: Because of the more extensive sampling and greater care in sample processing, as well as the more exacting method used for assessment of VAM infection, 1990 sample should be considered with more credence than the 1989 results. However, changes might have occurred due to the onset of the dry season.

There may be a problem with having so many variables in a single MANOVA while using the Hummel-Sligo procedure. If a single variable strongly affected by a factor creates a significant multivariate statistic, one might be led to assume other variables contributing little to the synthetic variables are also significant. There are, in fact, few truly independent

Figure 4: Root length, specific root length (SRL), and total mycorrhizal infection (HC), +/-1 standard error, for 1989 Edgecumbe root samples. Hatched boxes again represent plots with TSP added.



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variables in this MANOVA, most of the rooting parameters on one and infection indices in the other being closely hand procedure filters interrelated. The out these For treatment, which is the theoretical interrelationships. keystone of the experiment, the canonical loadings suggest two separate dimensions of effects: infection effects on one hand and branching effects on the other. It seems unlikely there is a problem in this case.

Compost treatment, TSP, block, and distance from stem all exhibited significant multivariate statistics (Table 8). This suggests univariate ANOVA's to be valid for each factor and variable.

Table 8: Multivariate and significant univariate F-statistic probability values from MANOVA of rooting parameters and mycorrhizal infection in 1990 Edgecumbe samples.

Factor	Parameter								
	Root length	Root weight	SRL	Branch- ing	Standard- ized root length	Standard- ized root weight	Mealybug capsules		
Treatment (COM)	-	-	-	.051	-	-	-		
TSP	-			-	-	-	_		
Block (BLC) –	-	-	-	-	-	<.001		
Distance from stem (DIS)	<.001	<.001	-	<.001	<.001	<.001	.009		
COM X TSP	-		-	-	-	-	.001		
COM X BLO	-			-		-	.012		
COM X DIS	-		-	-	.016	.027			
TSP X BLO	-	-	-	-	-	-	-		
TSP X DIS	-	-	-	-	-	-	-		
BLO X DIS	-	-	-	-	-	-	-		

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Table 8 continued

Factor		Parameter								
	cc	AC	ACC	THC	vc	HC	ACRL	IRL	trace)	
COM	.001	.026	.003	_	-	.006	-	_	.004	
TSP	<.001	<.001	<.001	-	-	<.001	-	-	.001	
BLO		-	-		-		-	.022	.001	
DIS	.004	.003	.009	.002	.035	<.001	<.001	<.001	<.001	
COM X TSF) —	-	-			-	-		.002	
COM X BLC) –	-	-	-	-		-	-	.469	
COM X DIS	5 -	-	-	-	-	-	-	-	.560	
TSP X BLC) –	-	-	-	-				.488	
TSP X DIS	; -	-	-	-	-	-		-	.007	
BLO X DIS	- 3	-	-	-	-	-	-	-	.735	

The interaction terms treatment X TSP and TSP X distance were also significant. The former was due completely to the occurrence of mealybug capsules. The latter is interesting, considering there were no significant univariate values. It could be the result of a series of extant, but undetected, TSP influences. Like compost, phosphate was applied as bands, and distance effects should occur.

TSP decreased mealybug capsule numbers when added to control or compost plots, but dramatically inflated them in filter mud plots (Figure 5). There were no overall differences in treatment, however. A threshold effect is possible, in which too much or too little phosphate both increase the occurrence of the pest.

Inorganic phosphate decreased the occurrence of coils and

Figure 5: Mealybug capsules (squared mean-root) per soil core, +/- 1 standard error, for the three treatments at Edgecumbe. Hatched boxes again represent plots with TSP added.



Treatment

arbuscules, and consequently total infection, but had no effect on the occurrence of hyphae or vesicles (Table 8, 9). Unlike the 1989 samples, TSP did not influence rooting parameters (Table 9). Block effects are discussed later (see "Block effects").

Table 9: The effect of triple superphosphate addition on root growth and mycorrhizal infection at Edgecumbe in 1990. Actual means are given.

Measure	Without TSP (N=90)	With TSP (N=45)
root weight / soil volume (g cm ⁻³)	0.00405	0.00453
root length / soil volume (cm cm ⁻³)	2.01	2.41
SRL (cm g^{-1})	623	596
Branches per cm root	2.21	2.13
CC (१)	24.3	8.68 A
AC (%)	16.4	11.4 A
ACC (%)	26.6	19.5 A
THC (%)	7.5	7.6
VC (%)	1.8	1.5
HC (%)	34.1	27.1 A

A: Significant TSP differences at p=0.05 level.

Combined treatment and distance influences on mycorrhizal infection are shown in Figures 6 and 7. Arbuscules alone were more prevalent in compost than filter-mud (p=0.012), or control plots (p=0.034), though the increase was marginally nonsignificant in the latter case. Combining arbuscules and coils overcomes this. Arbuscule/coil colonization was significantly greater in compost than in control (p=0.010) or filter mud (p=0.001) plots, as was total infection (p=0.002 and 0.016 Figure 6: Coil, arbuscular, vesicular, and intercellular hyphal colonization, +/- 1 standard error, of 1990 Edgecumbe root samples, taken at three distances from plant stems.



Figure 7: Total mycorrhizal infection (HC), and the frequency of root branching points, +/-1 standard error, of 1990 Edgecumbe root samples, at three distances from the plant stems.

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respectively). Total infection followed the same trends due to the relatively uncommon occurrence of hyphae and vesicles compared with coils and arbuscules.

Total infection increased from 5 cm distance away from the cane stalks to 35 cm (p=0.002) and 65 cm (p=0.016) (Figure 7). There was no difference between HC at 35 cm and 65 cm. Arbuscular, coil and arbuscule/coil colonization (p=0.004 and 0.020) each showed this trend (Figure 6).

Treatment X core interaction was not significant (Table 8; univariate p for ACC= 0.079). However, it is evident from Figures 6 and 7 that the 35 cm and to a lesser extent 65 cm distances were the major contributors to increased overall infection in compost plots. Using the 35 cm distance only to compare ACC of compost plots against control and filter mud plots gives p-values of 0.011 and 0.034 respectively. Using the 5 cm distance alone gives no significant differences.

Vesicular and intercellular hyphal colonization were not affected significantly by treatment (Table 8). Similar to coils and arbuscules, hyphae were less prevalent at 5 cm than 65 cm (p=0.001) and perhaps 35 cm (p=0.029). Vesicles, however, did not differ significantly between 5 and 35 cm or 5 and 65 cm, the only significant difference being a reduction at 35 cm compared to 65 cm (p=0.010) (Figure 6).

The frequency of root branching points, was significantly decreased in compost over control plots (p=0.017) (Figure 7). Each distance significantly varied from the others in its overall

branching mean (p<0.001 in each case).

Inspection of MANOVA standardized canonical coefficients for treatment shows the significant mycorrhizal infection indices, all of which are strongly based on the frequency of "active" infection units (arbuscule/coil), as the major contributors to one synthetic variable (canonical coefficients: CC = -0.540, AC=-0.363, ACC=-0.454, HC=-0.457, branching=0.289, THC=-0.232). Branching frequency and THC are the primary contributors to the synthetic variable (branching=-0.298, other THC=0.345, CC=-0.243, AC=-0.192, ACC=-0.281, HC=0.027). As with SRL in the 1989 samples, it then seems infection and branching are not causally related. The Pearson correlation of branching frequency and ACC on a per-sample basis is only 0.0118, very low compared to other variable correlations.

The apical ends of axes are lateral-free for some length, resulting in relatively greater overall branching frequency nearer the plant stem, (e.g. Christie 1975). Even controlling for this natural variation by looking at each distance separately does little to improve the correlation, although it is stronger at 35 cm (-0.505).

There remains the possibility that transverse hyphal colonization and branching points are related (Pearson correlation =-0.316), considering the canonical loadings. The correlation is stronger at 35 cm (-0.564) and 65 cm (-0.413), than at 5 cm (-0.049). THC was increased by compost addition (Figure 6), but the change was not significant (p=0.078).

As indicated in Table 8, effects of compost on root length, weight, and SRL were not significant. Distance effects are obvious: root growth decreased with increasing distance from the cane stalk. Standardizing the root weight and length of each coring distance as a percent of the total sample shows an interactive effect of treatment and distance (Figure 8) whereby compost-treated plants had relatively less root mass at the middle distance. While these interactions are significant in the univariate sense, the multivariate test statistic of treatment X distance (p=0.560) warns of a high probability of this trend being an artifact (Table 8).

Vesicular-arbuscular mycorrhizae (Windsor and Todds)

There were no significant compost effects on arbuscule/coil, arbuscular, hyphal, or vesicular colonization at Windsor (Two way, four-variable MANOVA; Pillai trace p=0.90).

At Todds (Five-way, six variable MANOVA), cultivar (Pillai trace p<0.001) and fertilizer (Pillai trace p=0.002) effects on colonization indices were significant and merited examination of separate ANOVA's for each variable. Treatment (Pillai trace p=0.26), distance from stem (Pillai trace p=0.077), and all twoway interaction effects were not significant. Univariate and multivariate significance values are outlined in Table 10.

Figure 8: Standardized root weight and length (amount in a single core as a percentage of the total in three cores), +/- 1 standard error, of 1990 Edgecumbe root samples.

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Factor		Overall (Pillai					
	сс	AC	ACC	THC	VC	HC	Trace)
Compost (COM) Cultivar (CUL) Fertilizer (FER Distance (DIS) Block (BLO)	- .002) - .044 -	- - . 009	. 004 _ . 005 _	.012	.035 .010 .000 _ _	.035 .008 	(.258) .000 .003 (.077)
COM X CUL COM X FER COM X DIS CUL X FER FER X DIS	- - - -	- - - -	.018 _ _ _	- - - -	- - .019 -	- - - -	(.151) (.174)

Table	10:	Signif	Eicant	univar	iate and	multivari	ate	F-statistic
I	probab	oility	values	from	variance	analysis	of	mycorrhizal
-	infect	ion in	dices a	t Todd	s.			

Separate ANOVA's for each infection index showed significantly higher CC, VC, ACC, and total mycorrhizal infection in roots of cultivar 80689 as compared to cultivar 62163 (Table 10, Figure 9). Elevating inorganic fertilizer application decreased hyphae and vesicle formation (Table 10, Figure 10).

Although the multivariate test statistics warn of a significant possibility of type I error when considering all indices, there are several significant treatment and distance effects in the univariate sense (Table 10). These values are here explored as possible trends rather than significant findings, especially compost effects, where the Pillai trace p=0.26.

Compost had a depressing effect on THC, VC, and total

Figure 9: Arbuscule/coil, intercellular hyphal, vesicular and total colonization, +/- 1 standard error, of composttreated and control plants at Todds. Hatched boxes represent cultivar 80689, open boxes cultivar 62163.



Figure 10: Total, arbuscule/coil, vesicular, and intercellular hyphal colonization of roots, +/- 1 standard error, for two fertilizer levels and sampling distances at Todds. Fertilizer levels are 133 kg N/ha (solid lines) and 193 kg N/ha (dashed lines).



infection (Figure 9). This is contrary to the hypothesized effect, and to effects evident at Edgecumbe. However, there was no significant depression of "active" infection: coils and arbuscules (Figure 9). The effect of sampling distance from plant stems was significant for CC, AC, ACC and HC, colonization increasing with distance in each case (Figure 10).

Soil Tests (Edgecumbe)

Neither treatment (Three-factor, three-variable MANOVA; Pillai trace p=0.44), nor TSP (Pillai trace p=0.46) significantly altered tested soil parameters (Table 11).

Table 11: Soil properties for the three treatments at Edgecumbe.

Treatment	N I	Loss-on- gnition	- SE (%)	Air-dry H ₂ O (%)	SE (Available (ug g ⁻¹ so	P SE ^A il)
Control							
+ TSP	5	7.8	0.37	1.26	0.19	12.2	1.00
- TSP	10	7.4	0.26	1.22	0.13	10.1	0.92
overall	15	7.6	0.21	1.24	0.11	9.64	0.69
Compost							
+ TSP	5	8.1	0.37	1.30	0.19	8.54	0.54
- TSP	10	7.6	0.26	1.32	0.13	9.26	0.86
overall	15	7.8	0.21	1.31	0.11	9.02	0.60
Filter mud							
+ TSP	5	7.6	0.37	1.23	0.19	16.9	7.81
- TSP	10	7.7	0.26	1.29	0.13	9.57	0.61
overall	15	7.7	0.21	1.27	0.11	12.0	2.61
A. Data was	in	orse tra	neform	ed for M	ANOVA	Actual	not pooler

": Data was inverse transformed for MANOVA. Actual, not pooled, SE's are given.

Block effects were strongly significant, however. (Pillai trace p<0.001) (Figure 11). Univariate F-tests for block effects were therefore calculated for loss on ignition (p=0.001), air-dry H_2O (p=0.001), and available phosphorus (p=0.071).

Block effects (Edgecumbe)

Block effects were often significant, as expected from such a large experimental area. In most instances, blocking was merely intended to reduce residual variability and had no hypothetical constraints attached to it. Several block effects were explored further on the assumption that the slope might affect cane plants in consistent ways (Figures 11-13).

The hypothesis that compost might improve tillering more on sloped than on flat areas (by preventing erosion of fertilizer) was tested by comparing the six "flat" and three "sloped" blocks. In fact the opposite was true. On flat areas compost (p=0.004) and filter mud (p<0.001) improved tillering per metre row, but on sloped areas neither did (p=0.193 and 0.127 respectively) (Figure 11, all blocks are not shown). This could, however, be a type II error caused by the smaller sample number of sloped plots. Similar contrasts were calculated for tillering per plant, with no significant results.

The assumption that compost addition would improve tillering more in poor areas also seems untrue, considering the nil effect of compost on the poorly-tillering 40 m block (Figure 11). If compost preferentially improved poor areas one would expect

Figure 11: Vertical profile of the Edgecumbe field (horizontal and vertical axes are not to scale), showing position of blocks and soil properties, +/-1 standard error, along the toposequence. The 0 m, 0 m position is arbitrary (access road).



Figure 12: Variation in tillering along the toposequence at Edgecumbe. Bars represent +/- 1 standard error.

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Figure 13: Effect of the toposequence at Edgecumbe on IRL and mealybug capsules per soil core, +/-1 standard error.

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decreased tiller variance in compost plots. This was not true on either a per plant or per metre row basis (Bartlett Chi-Square test; p=0.068 and 0.762 respectively).

To assume consistent slope effects, and overcome possible concomitance of slope and other environmental factors, would require much more extensive sampling. However, sloped blocks did have more mealybug capsules (p=0.001) and infected root-length (p=0.007) than flat blocks (Figure 13), perhaps due to increased organic matter and moisture content (Figure 11).

CHAPTER 4: Discussion

Mycorrhizal Infection

Compost application stimulated VAM infection of sugarcane roots under certain conditions only. The effect varied with specific fungal structures (stimulation only of the coil/ degrading coil/ arbuscule association), parts of the plant root system, and experimental fields.

There are several possible explanations for VAM infection response to compost at Edgecumbe but not Windsor or Todds. (a) Field differences in rainfall or soil could be controlling factors, although compost is beneficial in a wide range of sites (de Boer, 1989). Todds is located in an area of higher rainfall than is Edgecumbe, for example (Vernon and Carroll, 1965). (b) The Edgecumbe field was plant cane whereas the others were second ratoon. Yield, and presumably other, effects diminish in ratoons, as compost is not reapplied each year. (c) Sampling at Edgecumbe was a rigorous process acquiring total roots to 21 cm Due to the cemented nature of the clay soil, the use of a depth. trowel at Todds and Windsor tended to recover fewer small laterals, from shallower depth. New roots may be preferential sites for VAM infection (e.g. Jodice and Nappi, 1987), and the presence of a cane trash mulch under ratoon crops may have had such a stimulatory effect on VAM that it drowned out any residual compost effect. (d) The sampling times were different. Edgecumbe was sampled at the end of the wet season, the other two in the dry season. Windsor and Todds were also sampled after harvesting, albeit soon afterward, and root senescence could have been a factor. (e) Type I or II error are possible.

Considering the rapid turnover of organic matter in the Tropics and the application rate of 5 t ha^{-1} , a level considered too small to be beneficial in most tropical settings (Dalzell et al., 1987), the residual compost value to ratoon crops would seem to be very small. Treatment loss-on-ignition differences were not detected only eighteen months after compost banding. However, applied compost was less than 0.4% of soil weight to 20 cm depth, and loss on ignition standard errors were around 0.3%. Considering soil heterogeneity, the failure to detect differences with this sampling scheme is not surprising, and does not really suggest that compost was mostly decomposed by the time of It should also be noted that loss-on-ignition values sampling. may not be directly indicative of absolute organic matter levels because of the presence of volatile calcium carbonate. That is, organic matter levels may not have been as high as 7-8%.

Improvement of ration yields could result from lasting soil structural benefits, which were not examined. The lack of significant differences in loss-on-ignition or air-dry H_2O suggest, somewhat, that this was not the case. Stimulation of plant cane VAM infection could also lead to increased soil spore density, in turn leading to increased VAM infection or establishment rate in rations. Senescing roots can also serve as VAM inocula (Harley and Smith, 1983). However, as no significant
compost-VAM connections were found in ratoon crops, and spore counts were not undertaken, such hypotheses cannot be given much credence. Benefits of the mycorrhizal symbiosis may decline with perennial plant age in any case (Douds and Chaney, 1986).

In the Todds ratoon crop, compost treatment tended to lower plant VAM infection. This was opposite to the trend at Edgecumbe, but multivariate tests were nonsignificant, and it was confined to vesicles and hyphae, not arbuscules. Vesicles are indicative of older, less active infection (Douds and Chaney, 1986).

Mycorrhizal infection was less in roots near plant stalks compared to more distal roots, and stimulation by compost was significant only in the distant roots. This could have resulted from preferential infection of young rootlets, as are proportionately more frequent further from the stems. NK fertilizer suppression of mycorrhizal infection to a minimum threshold (e.g. Anderson et al., 1987; Table 1), thereby damping out any stimulatory effect of compost, could also account for the distance effect.

If the latter is true, the particular application process of compost and fertilizer may be key to understanding patterns of compost-mediated VAM stimulation in different parts of the root systems. Inorganic fertilizer was applied in narrower bands than compost, creating a spatial mosaic whereby compost and fertilizer were both present to about 8 cm from the stem, compost alone from 8 to 15 cm, and no addition beyond. The heterogeneous banding pattern may allow compost stimulation of VAM in parts of the root system even if this can be nullified by NK fertilizer. Broadcast fertilizer would be less advantageous.

The three coring distances should have roughly sampled each of these effect bands. The 30 cm core was beyond the compost band as applied, but with settling and nutrient mobility, bands should become wider and less consistent with time. Infection stimulation through compost addition occurred even at 65 cm, due perhaps to settling or cross-inoculation from one part of the root system to another.

Examination of fertilizer-level trials at Todds was undertaken in part to elucidate the role of the NK fertilizer band. Although the separate experiments are not strictly comparable for reasons noted above, results tend to contradict the "mosaic banding" hypothesis. Increasing the fertilizer rate only diminished hyphae and vesicles, while coils and arbuscules again decreased (nonsignificantly) with proximity to the stem. Either there is another controlling factor related to stem proximity, or infection has a minimum threshold, being not further decreased by fertilizer in excess of a certain level.

VAM benefits?

Compost application certainly led to improved sugarcane nutrition at Edgecumbe, as indicated by the tissue phosphorus content, yield, and tillering data, and it did so without noticeably exaggerating pest (mealybug) or weed problems. Improved

tillering with compost application resulted from increased stems per plant rather than improved sprouting. Few areas of poor sprouting were observed anywhere in the field. Tillering benefits therefore probably accrue from nutritional rather than soil-physical effects. Grass tillering is often associated with phosphorus nutrition (e.g. Hackett, 1968).

It is a tenuous leap between documenting VAM increases and assuming consequent plant benefits in the field (Fitter, 1985b), but VAM stimulation is likely to be one cause of compost benefits at Edgecumbe for several reasons.

Firstly, the fungal structures most stimulated were intracellular arbuscules and hyphal coils. Although direct evidence is lacking, these are generally assumed to be the sites of host-endophyte phosphorus transfer because of the extensive surface area of contact between fungus and plant cytoplasm, and because arbuscules are short lived (Harley and Smith, 1983). It should be stressed again that observed structures other than arbuscules may not have been mycorrhizal.

The Edgecumbe field also seemed to be phosphorus deficient for cane. The mycorrhizal association is most beneficial to plants in such situations (Chapter 1). Leaf phosphorus content in control plots was only 0.118%, well below the average BSIL test value of 0.17% (BSIL Agronomic Committee, 1986). As well, TSP has seemed to stimulate yield in an adjacent, non striptilled field (ARU unpublished data). Fitter (1985b) warns that mycorrhizae can be parasitic if they cause carbohydrate limitation, but this would be difficult to attain in a carbohydrate-rich crop like sugarcane, and the 0.132% leaf phosphorus value of compost plots is still below the 0.15-0.2% level considered necessary for optimal growth on other Caribbean islands (BSIL Agronomic Committee, 1986).

Barbados has a distinct dry season, during which root sampling was undertaken. VAM is likely to be advantageous to plants grown in dry conditions since phosphate diffusivity increases with moisture (Cooper and Tinker, 1981).

Finally, compost and filter mud application led to increased leaf phosphorus levels. Triple superphosphate, which severely decreased infection where added, did not significantly affect tillering or leaf phosphorus. It may simply have had a smaller and less detectible effect since, considered alone, control plots with TSP were not significantly less tillered than compost plots. Inorganic phosphate fertilizer alone was insufficient to stimulate sugarcane P uptake, or at least was less efficient than compost or filter mud. The simple P-fertilizer value of compost may therefore not be the principal cause of improved yield.

The total amount of phosphorus in the compost is barely adequate to account for observed yield benefits. Using an average content of 2.6% P_2O_5 (Table 1), about 45 kg P ha⁻¹ was applied to experimental fields as compost. Assuming stems to contain about 0.35% P (Chang-Yen et al., 1983), this addition would be enough to produce an extra 13 t ha⁻¹ cane, without considering increased P content of leaves. This amount of P

could account for observed yield benefits in some sites (de Boer, 1989), assuming unusually high recovery rates (plant plus ratoon crops) of over 50%. It could not completely account for the yield benefit over several years at some sites, such as Windsor. Either compost influences P uptake in other ways, or P is not the key limiting factor in these sites.

The compost is a source of other nutrients. However, experiments have suggested that NK fertilizer applications are optimal (de Boer, 1989). Compost is not directly substitutable for fertilizer, for it only increases yield of sugarcane given recommended or inflated NK fertilizer doses (de Boer, 1988b).

There is, however, a fundamental difference between organically-complexed and inorganic N, P and K. The slow release of the organic nutrients may offset losses by leaching or phosphorus fixation.

Filter press mud had affected cane tillering and tissue phosphorus in similar ways and extents as compost, without any pronounced stimulation of VAM. However, neither did it suppress VAM infection like TSP. Total P applied as filter mud was greater than that applied as compost or TSP. Although not analyzed in this experiment, filter mud commonly has a total phosphorus content of 0.45 to 3.8% of dry matter (Prasad, 1976a; Chang-Yen et al., 1983). This is comparable to levels in the bagasse-based compost used here (Table 1: elemental P of compost is 0.9 to 1.4% dry matter). Assuming 60% moisture content (Moberly and Meyer, 1978; Prasad, 1976a) the P-rate from filter

mud would have been, very roughly, 200 kg ha⁻¹. This high level could account for the lack of mycorrhizal stimulation in filter mud plots.

In Trinidad, filter-press mud is not considered an equally efficient P-fertilizer to TSP (Cooper and Abu Idris, 1980). Considering application rates, the BSIL compost appears to be more efficient than either TSP or filter-press mud in Barbados, perhaps due to its VAM stimulating properties. In South Africa, 3 t ha⁻¹ of a filter press cake compost had a yield stimulation equivalent to 45 t ha⁻¹ of fresh filter cake (Moberly and Meyer, 1978). The yield trends under these different phosphorus sources should become clearer in the three ratoon crops.

Certainly the compost was a phosphorus source, but this does not preclude the existence of mycorrhizally-mediated benefits as well. VAM are extremely effective at recovering P from poorlysoluble sources like organic matter or "fixed" phosphate (Chapter 1), so improved uptake of phosphorus in compost-treated plants may be a combined result of source and pathway stimulation. Compost is also a micronutrient source (Table 1), and has a plethora of potential benefits (Chapter 1). To narrow these down to a single factor is neither feasible nor logically justifiable. The value of these findings lies in demonstration of the potential for mycorrhizal benefits, under field conditions.

Other potential benefits of this specific compost, aside from those mentioned in Chapter 1, may be functions of its constituents. The particular constituents have been studied separately, in varying environmental contexts and application rates. Fly ash, composed principally of SiO_2 , can increase phosphorus availability (Pan et al., 1977), perhaps by decreasing P fixation (Reeve and Sumner, 1970), and can also alter soil water conductivity (Chang et al., 1977) and micronutrient availability (Plank and Martens, 1973). Bagasse is probably beneficial only at very high application rates as a mulch, under dry conditions (Nkrumah et al., 1982).

Filter mud, or filter cake, can improve cane yield (Prasad, 1976a; Moberly and Meyer, 1978). Porosity and water holding capacity can be altered by broadcast rates of only 15-30 t ha⁻¹ (Paul, 1974), and microflora stimulated by 10-20 t ha⁻¹ (Arcia et al., 1987). It can provide micronutrients (Kapur and Kanwar, 1989), but is primarily a phosphorus source interchangeable with TSP (Prasad, 1976a).

The study of Prasad (1976a, 1976b) provided a series of results roughly corresponding to those of the present study and the Barbados composting project in general. In Trinidad, filter mud application increased sugarcane yield and leaf phosphorus content (Prasad, 1976a, 1976b), showing occasional residual benefit in ratoons (Cooper and Abu Idris, 1980). Filter mud also allowed improved response to nitrogenous fertilizer. Filter mud and TSP were interchangeable, however TSP did not inflate leaf phosphorus as efficiently as filter mud. Prasad attributed the last to more soil fixation of TSP-phosphorus than filter mudphosphorus. An alternate explanation might be more suppression

of VAM by TSP than by filter mud. The two possibilities are difficult to separate causally because of their own interconnectedness. In Prasad's study, the lowest mud application rate was 20 t ha⁻¹.

The observed stimulation of VAM by compost could have resulted from factors other than those VAM-organic matter relationships outlined in Chapter 1. The compost could conceivably have been an inoculum (Warner, 1984), or the altered soil environment caused qualitative changes in the mycorrhizal flora, shifting the population balance towards a more highly infective species (Borie and Zunino, 1983; Harley and Smith, 1983). The use of strip tillage may have been conditionally vital to improved VAM status, slowing soil organic matter breakdown (Hayman, 1987).

Percentage infection can be a function of root growth rates (Harley and Smith, 1983). However, in this experiment no root length or infected root length differences were detected across treatments. Snapshoting a single point in time with "percent infection" also fails to give a dynamic account of mycorrhizal activity. Infection is not only a function of the number of infection units and their lateral extension along roots, but also of turnover time. When assessing infection, distinguishable hyphae (including hyphae composing arbuscules) were considered necessary for a successful intersection to be counted. Diffusely stained areas assumed to consist of near-to-completely degraded hyphae were commonly observed. Including these diffusely stained

areas as part of total infection eliminated the significant compost effect. If they do represent formerly "active" infection points, their compensation for increased AC and CC suggests they are perseverent, and that compost acts on VAM not by increasing infection points but by extending the time between initiation and complete degradation of arbuscules and coils. This was not included in the analyses because of the great uncertainty factor involved in counting these diffusely stained areas. The hypothesis is supported by the lack of treatment differences in vesicle formation along with coils and arbuscules. Vesicles are commonly prevalent in the late stages of infection (Douds and Chaney, 1986).

Root Growth

The two sampling phases at Edgecumbe are not strictly comparable because of methodological differences, but gave generally consistent results. Neither phase showed significant compost effects on total root length, weight, or SRL. Root branching frequency and standardized length were calculated only in the second phase. The only contradictory effect was the significant TSP influence on root length and SRL in 1989 (Figure 4).

The lack of differences in infected root length of TSP and non-TSP treated plants in 1989 resulted from the compensation of stimulated root length for suppressed infection. One of the original experimental hypotheses was that plants with low mycorrhizal infection would require lengthier, more fibrous and ramified root systems than strongly VAM plants. This would seem to be the case in TSP plots where mycorrhizal infection was decreased, but the correlation between infection and SRL was weak on a per plant basis. While high correlation would not prove causality given the wide range of interconnected treatment effects, a low correlation certainly makes it unlikely.

Obviously, soil phosphorus levels are also a factor in root ramification. Phosphorus fertilization, as noted in Chapter 1, has variable effects on root length and SRL. In general it will decrease SRL in soils with adequate plant-available phosphorus (Anghinoni et al., 1980; Hetrick et al., 1988). In phosphorus deficient conditions, as has been suggested for this field, phosphorus can increase SRL (Price et al., 1986), and this may have been the operative mechanism in TSP plots.

Although TSP addition must have raised soil-P somewhat, this was undetected. By the time soil samples were taken, most of the phosphate may already have become fixed into unavailable forms, but still somehow suppressed VAM.

With compost addition, root branching points tended to be spaced further apart. This measure could represent two distinct differences in root architecture: a decrease in the distance between laterals of the same order (link length), or a topological alteration in the branching pattern and number of higher order laterals. The former is more likely to be the case since a lowered proportion of finer, high order laterals should also lead to decreased SRL. This did not occur.

In either case, decreased branching of compost-treated root systems can result in exploration of a greater soil volume than by the same mass of control plant roots (see Fitter, 1987). Well-spaced roots will be less likely to have overlapping depletion zones. Compost treated plants' ability to recover water and mobile nutrients should therefore be bolstered.

Phosphorus is relatively immobile, and root length alone controls uptake (Fitter, 1987) unless a plant is strongly mycorrhizal. By proliferating hyphae into soil and transporting phosphorus to roots, VAM make phosphorus functionally mobile (Hetrick et al., 1988). In combination with VAM, root topology can then alter plant-accessible phosphorus and mobile nutrients. The combination of mycorrhizal stimulation and decreased root ramification could be advantageous in nutrient-limited or waterlimited situations, as commonly occur in the dry season.

A caution should be added. Since "branching" was not a topological assessment of entire roots, certain assumptions were made. There could not be more apical ends of axes in cores of one treatment, since there tends to be a delay before lateral initiation behind extending root tips (e.g. Christie, 1975). As a generalization of this case, there could not be any regular change in branching frequency along axes, combined with treatment-induced extension rate differences. Since samples were taken by coring at regular distances rather than excavating whole plants, this would mean different sections of root systems were sampled for each treatment. The lack of treatment differences in

root weight or length in each core suggest constant axial growth rates. There were core differences in branching, but these could be effects of the fertilizer/compost banding system. Studies of barley (Hackett, 1968; Drew and Saker, 1978), mulga, Mitchell, and buffell grasses (Christie, 1975), and cotton (Price et al., 1986) have shown phosphorus fertility to not affect, or affect only slightly, axial extension rates. Christie's study (1975) also found mean extension and initiation rates, though altered by soil fertility, to be constant for each root system component (axes, first order laterals, second order laterals). It seems probable that branching frequency as tested here indicated true localized differences resulting from experimental treatments.

Finally, the use of branching frequency as an index of total soil volume explored by roots is based on an assumption that, once initiated, laterals have constant, equal extension rates, as supported by Christie (1975). Branching frequency is a rough measure, and with several hypothetical root arrangements a lower value does not necessarily correlate to exploration of more soil. All such architectural analyses have assumptions (Fitter, 1987), and examination of complete root systems in the field, especially in clay soils, is prohibitive. The suggested operative effect here is link length rather than lateral initiation, however, a conceptually simpler effect.

Observed branching effects might be simply due to soil fertility or structural differences such as altered water-holding capacity. Again, interpretation is made complex by the combined

influences of several nutrients and environmental conditions. However, in low-P soils, P-fertilization should increase root ramification (e.g. Price et al., 1986). This was the case with SRL in the 1989 samples. Strangely (if one assumes SRL and branching to be functionally equivalent), compost had an opposite effect on proliferation. It does not act as a simple P-source, and its mycorrhizal stimulating property is the most appealing explanation.

When confronted with a heterogeneous soil environment, plants will proliferate fine laterals into nutrient (phosphorus) rich pockets (Drew and Saker, 1978; Anghinoni et al., 1980). While the fertilizer-free 65 cm core did have the lowest branching, this could have been due to the presence of axial terminals. The greatest treatment differences were at 35 cm. Control plots actually had the highest branching, indicating that compost-P did not cause increased ramification.

Compost treated plants also had relatively more (nonsignificant trend) of their root mass in the 5 cm core. Root growth leveled off after the 5 cm core rather than smoothly decreased as in control plants (Table 8). Differences in relative root allocation if not absolute growth with distance are suggested.

Examination of Figure 7 immediately suggests a relationship between branching and mycorrhizal infection, but the low persample correlations make a causal relationship seem unlikely indeed, even considering the residual noise associated with all

the different fertilizer additions. The canonical coefficients for treatment suggest separation of branching effects from most indices of VAM infectivity, THC being the exception. There remains a good possibility of intercellular hyphal colonization and branching frequency being related.

As with SRL in the 1989 samples, a direct connection between VAM infection and root architecture beyond the fact that both are altered by experimental treatments, is not well supported. If mycorrhizae were a factor controlling root branching, one must assume the large amount of residual error created by so many treatment combinations drowned out any evident correlation, or the conflicting, circular influences of organic matter on VAM, organic matter on root branching, and VAM on root branching were simply too complex to be clear in a non-manipulative study such as this.

<u>Miscellany</u>

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Moberly and Meyer (1978) found a filter cake compost to be beneficial to sugarcane growth in low yielding areas only. Although examination of this phenomena here involved only heterogeneous areas of a single field, and used tillering as an index of yield, there was no such trend. Day et al. (1987) found a toposequence to affect mycorrhizal infection. Again, the scale was much less here and slope effects were probably limited to soil-moisture, but no such trend was evident.

Excess phosphate fertilization may be detrimental to cane

growth (Yates, 1964). TSP application in filter mud plots seemed to stimulate the amount of mealybug capsules, and perhaps decrease cane tillering. The type of phosphorus, in concert with application rate, may become necessary to consider if additions greater than those presently in practice are attempted.

CHAPTER 5: Conclusion

In answer to the hypotheses presented in Chapter 1:

a) Compost application does improve leaf phosphorus content, tillering, and probably yield of sugarcane in Barbados.

b) Compost increases root infection by the intracellular coil/ arbuscule association of VAM, but only in certain situations. It may do so only in plant cane. Filter mud does not stimulate VAM infection, while triple superphosphate decreases it.

It cannot definitely be stated that yield increases arise from ecological mechanisms other than the fertilizer value of the compost (i.e. stimulation of mycorrhizal infection). However, coincidental evidence (see Chapter 4) implicates VAM as one contributor to yield benefit.

c) No evidence shows compost to be most beneficial in areas of low tillering.

d) No differences were detected in compost effects or VAM infection along a slight slope. There was no evidence of compost aiding plant growth by preventing fertilizer loss as runoff.

e) Compost application did lead to altered root architecture, without absolute differences in root length, weight, or SRL. Branching was decreased by compost addition. What this means, exactly, is not certain given field constraints on sampling. However, the suggested mechanism is a reduction of internal link length by compost, leading to better, more even soil exploration by root systems. Whether this is a result of stimulated VAM or another, perhaps edaphic, effect of compost is uncertain. The lack of increased root mass along with the increased cane yield from compost application also suggests that compost-treated plants may have had lower root/shoot ratios, and therefore a better proportional allocation of carbon to photosynthetic tissues.

The value in this work lies in several features. Firstly, it was a field study. The results do not require a series of assumptions for extrapolation to this particular ecologicalgeographical context. One goal of the strip-plot trials initiated by BSIL has been to make their results readily applicable to real farm situations (de Boer and Hudson, 1987). This aim was preserved in designing the present study.

The stimulation of VAM infection with such a small addition of organic matter is unusual, and may be dependent on the low ambient organic matter levels in the soil tested.

Several possible mechanisms vital to observed yield benefits of compost addition are suggested. Firstly, the heterogeneous banding pattern of compost and NK fertilizer should be maintained, or perhaps exaggerated. Spreading the compost over a wider area might further stimulate root infection, and perhaps result in wider architectural changes. Compost may be of most use in phosphorus-deficient and dry areas due to these effects on VAM and roots. The compost may be a more efficient phosphorus source, in terms of total P content, than filter mud, and if the added cost of composting is not great, should be preferred due to

its other effects on the plant-soil environment. Compost is a better, and cheaper, source of P than triple superphosphate.

3

More extensive studies with a gradient of compost, TSP, and filter mud levels would be valuable in further examining observed effects, and testing some of the hypothesized explanations given in the previous chapter. Items of specific interest might be: the relative phosphorus-recovery curves of distinct phosphorus sources; the presence of minimum or maximum infection thresholds and whether these are affected differentially by phosphorus from distinct sources; any confounding influence of water; and the residual ratoon effect and whether there is any mycorrhizal carryover from one year to another, perhaps through spores. What would seem to be a vital study component- a first ratoon cropwas not included in the three fields examined here. Having already found plant cane VAM stimulation at Edgecumbe, it would be a good candidate to follow through the ratoons. Coincident laboratory studies might elucidate the mycorrhizal role in yield benefit.

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REFERENCES

- Abbott, L. K., and A. D. Robson. 1979. A quantitative study of the spores and anatomy of mycorrhizas formed by a species of <u>Glomus</u> with reference to its taxonomy. <u>Aust. J. Bot.</u> 27: 363-375.
- Abbott, L. K., A. D. Robson and G. de Boer. 1984. The effect of phosphorus on the formation of hyphae in soil by the vesicular-arbuscular mycorrhizal fungus, <u>Glomus</u> <u>fasciculatum</u>. <u>New Phytol.</u> 97: 437-446.
- Adams, T. McM., and R. J. Laughlin. 1981. The effects of agronomy on the carbon and nitrogen contained in the soil biomass. J. Agric. Sci. 97: 319-327.
- Allen, M. F., T. S. Moore, Jr. and M. Christensen. 1980. Phytohormone changes in <u>Bouteloua</u> <u>gracilis</u> infected by vesicular-arbuscular mycorrhizae: I. Cytokinin increases in the host plant. <u>Can. J. Bot.</u> 58: 371-374.
- Anderson, E. L., P. D. Millner and H. M. Kunishi. 1987. Maize root length density and mycorrhizal infection as influenced by tillage and soil phosphorus. <u>J. Plant. Nutr.</u> 109: 1349-1356.
- Anghinoni, I., and S. A. Barber. 1980. Phosphorus influx and growth characteristics of corn roots as influenced by phosphorus supply. <u>Agron. J.</u> 72: 685-688.
- Arcia, F. J., Y. Amoros and L. A. Mustelier. 1987. Influence of the press-mud-cake application on some biological properties of three typical Cuban soils. In: J. Szegi, ed. <u>Proceedings</u> of the Ninth International Symposium on Soil Biology and <u>Conservation of the Biosphere.</u> Budapest: Akadémiai Kiado, pp. 473-482.
- Bandyopadhyay, S. K., and R. De. 1986. Nitrogen relationships and residual effects of intercropping sorghum with legumes. J. Agric. Sci. Camb. 107: 629-632.
- Barbados Sugar Industry Limited Agronomic Committee. 1986. Leaf analysis 1985. <u>BSIL Agronomy Research Unit Bulletin.</u> Number 47.
- Barker, H. R., and B. M. Barker. 1984. <u>Multivariate Analysis of Variance (MANOVA): A Practical Guide to Its Use in Scientific Decision Making.</u> Alabama: University of Alabama Press.

- Baylis, G. T. S. 1975. The magnoliad mycorrhiza and mycotrophy in root systems derived from it. In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. <u>Endomycorrhizas: Proceedings of a</u> <u>Symposium held at the University of Leeds, 22-25 July, 1974.</u> London: Academic Press, pp.373-389.
- Bethlenfalvay, G. J., J. M. Ulrich and M. S. Brown. 1982. Plant response to mycorrhizal fungi: Host, endophyte, and soil effects. <u>Soil Sci. Soc. Amer. J.</u> 49: 1164-1168.
- Black, R., and P. B. Tinker. 1979. The development of endomycorrhizal root systems. II. Effect of agronomic factors and soil conditions on the development of vesiculararbuscular mycorrhizal infection in barley and on the endophyte spore density. <u>New Phytol.</u> 83: 401-413.
- Boerner, R. E. J. 1986. Seasonal nutrient dynamics, nutrient resorption, and mycorrhizal infection intensity of two perennial forest herbs. <u>Amer. J. Bot.</u> 73: 1249-1257.
- Borie, F., and H. Zunino. 1983. Organic matter-phosphorus associations as a sink in P-fixation processes in allophanic soils of Chile. <u>Soil Biol. Biochem.</u> 15: 599-603.
- Brundrett, M. C., Y. Piche and R. L. Peterson. 1984. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. <u>Can. J. Bot.</u> 62: 2128-2134.
- Buttery, B. R., S. J. Park, W. I. Findlay and B. N. Dhanvantari. 1988. Effects of fumigation and fertilizer on growth, yield, chemical composition, and mycorrhizae in white bean and soybean. <u>Can. J. Plant Sci.</u> 68: 677-686.
- Chang, A. C., L. J. Lund, A. L. Page and J. E. Warneke. 1977. Physical properties of fly ash-amended soils. <u>J. Environ.</u> <u>Qual.</u> 6: 267-270.
- Chang, J. F., and R. M. Shibles. 1985. An analysis of competition between intercropped cowpea and maize II. The effects of fertilization and population density. <u>Field Crops Res.</u> 12: 145-152.
- Chang-Yen, I, P. L. Bodoe and R Mohammed. 1983. Chemical analysis of seven nutrient elements in some sugar-cane products and by-products. <u>Trop. Agric. (Trinidad)</u> 60: 41-43.
- Chapin, F. S. 1980. The mineral nutrition of wild plants. <u>Ann.</u> <u>Rev. Ecol. Sys.</u> 11: 233-260.

Christie, E. K. 1975. Physiological responses of semiarid grasses. II. The pattern of root growth in relation to external phosphorus concentration. <u>Aust. J. Agric. Res.</u> 26: 437-446.

- Cooper, B. R., and E. A. Abu Idris. 1980. Sugarcane response to filter application on Trinidad soils. In: <u>International</u> <u>Society of Sugarcane Technologists: Proceedings XVII</u> <u>Congress. 1-11 Feb. 1980. Manila, Philippines.</u> Vol. 1, pp. 220-232.
- Cooper, K. M., and P. B. Tinker. 1981. Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. IV. Effect of environmental variables on movement of phosphorus. <u>New</u> <u>Phytol.</u> 99: 327-339.
- Cox, G., F. G. Sanders, P. B. Tinker and J. A. Wild. 1975. Ultrastructural evidence relating to host-endophyte transfer in a vesicular-arbuscular mycorrhiza. In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. Endomycorrhizas: Proceedings of a Symposium held at the University of Leeds, 22-25 July, 1974. London: Academic Press, pp. 297-312.
- Crawford, J. H. 1983. Composting of agricultural wastes- a review. <u>Process Biochem.</u> 18: 14-18.
- Daft, M. J., and T. H. Nicholson. 1969. Effect of Endogone mycorrhiza on plant growth. II. Influence of soluble phosphate on endophyte and host in maize. <u>New Phytol.</u> 68: 445-452.
- Daft, M. J., and T. H. Nicholson. 1966. Effect of Endogone mycorrhiza on plant growth. <u>New Phytol.</u> 65: 343-350.
- Dalzell, H. W., A. J. Biddlestone, K. R. Gray and K. Thurairajan. 1987. <u>Soil Management: Compost Production and Use in</u> <u>Tropical and Subtropical Environments.</u> Rome: FAO Soils Bulletin 56.
- Day, L. D., D. M. Sylvia, and M. E. Collins. 1987. Interactions among vesicular-arbuscular mycorrhizae, soil, and landscape position. <u>Soil Sci. Soc. Amer. J.</u> 51: 635-639.
- de Boer, H. G. 1989. The more fertiliser the more yield? In: <u>Barbados Sugar Technologists Association: Proceedings of the</u> <u>Seventh Annual Conference</u>, November 22 and 24, 1989. pp. 27-31.
- de Boer, H. G. 1988a. Fertilizer facts. <u>BSIL Agronomy Research</u> <u>Unit Bulletin.</u> Number 64.

- de Boer, H. G. 1988b. Results of Experiments 1988. <u>BSIL Aqronomy</u> <u>Research Unit Bulletin.</u> Number 61.
- de Boer, H. G. 1986. Development of a system of strip trials in Barbados sugar cane. In: <u>International Society of Sugarcane</u> <u>Technologists: Proceedings XIX Congress. 21-31 August 1986.</u> Jakarta, Indonesia. pp. 41-51.
- de Boer, H., and C. Hudson. 1987. Developing strip tillage to reduce cultivation costs. <u>Sugar y Azucar.</u> 55: 30-34.
- Del Zan, F., L. Baruzzini, M. Candiotti, I. Tonetti and G. Murgut. 1987. Manuring a maize crop with composts obtained from different technological processes: short term effects on soil-plant system. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production, Quality, and Use.</u> London: Elsevier Applied Science, pp. 546-555.
- Dighton, J., E. D. Thomas and P. M. Latter. 1987. Interactions between tree roots, mycorrhizas, a saprotrophic fungus and the decomposition of organic substrates in a microcosm. <u>Biol. Fertil. Soils</u> 4: 145-150.
- Douds, D. D., and W. R. Chaney. 1986. The effect of high nutrient addition upon seasonal patterns of mycorrhizal development, host growth, and root phosphorus and carbohydrate content in <u>Fraxinus pennsylvanica</u> Marsh. <u>New Phytol.</u> 103: 91-106.
- Drew, M. C., and L. R. Saker. 1978. Nutrient supply and growth of the seminal root system in barley. III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. J. Exp. Bot. 29: 435-451.
- Ewel, J. J. 1986. Designing agricultural ecosystems for the humid tropics. <u>Ann. Rev. Ecol. Syst.</u> 17: 245-271
- Fitter, A. H. 1987. An architectural approach to the comparative ecology of plant root systems. <u>New Phytol.</u> 106 (Suppl.): 61-77.
- Fitter, A. H. 1985a. Functional significance of root morphology and root system architecture. In: A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher, eds. <u>Ecological Interactions in</u> <u>the soil: Special Publication of the British Ecological</u> <u>Society, No. 4</u>. Oxford: Blackwell, pp. 87-106.
- Fitter, A. H. 1985b. Functioning of vesicular-arbuscular mycorrhizas under field conditions. <u>New Phytol.</u> 99: 257-265.

Friedrichsen, J., and C. C. Wei. 1969/1970. <u>Annual Report of the</u> <u>Taiwan Sugar Experimental Station.</u> 1969/1970: 22-33.

1/2

- Gianazzi-Pearson, V., and S. Gianazzi. 1983. The physiology of vesicular-arbuscular mycorrhizal roots. <u>Plant and Soil</u> 71: 197-209.
- Giovannetti, M., and B. Mosse. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. <u>New Phytol.</u> 84: 489-500.
- Godden, B., M. Marechal, X. Vekemans and M. Pennincky. 1987. Effects of manure compost on soil microbiological properties. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production, Quality, and Use.</u> London: Elsevier Applied Science, pp. 473-478.
- Gooding, E. G. B., A. R. Loveless and G. R. Proctor. 1965. <u>The</u> <u>Flora of Barbados.</u> London: Her Majesty's Stationery Office.
- Guidi, G., and G. Poggio. 1987. Some effects of compost on soil physical properties. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production</u>, <u>Quality, and Use.</u> London: Elsevier Applied Science, pp. 577-583.
- Hackett, C. 1968. A study of the root system of barley. I. Effects of nutrition on two varieties. <u>New Phytol.</u> 67: 287-299.
- Halliday, D. J. 1956 <u>The Manuring of Sugar Cane.</u> Geneva: Centre d'etude de l'azote.
- Harley, J. L., and S. E. Smith. 1983. <u>Mycorrhizal Symbiosis</u>. London: Academic Press.
- Hayman, D. S. 1987. VA Mycorrhizas in field crop systems. In: G. R. Safir, ed. <u>Ecophysiology of VA Mycorrhizal Plants.</u> Boca Raton: CRC Press, Inc., pp. 171-192.
- Hayman, D. S. 1975. The occurrence of mycorrhiza in crops as affected by soil fertility. In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. <u>Endomycorrhizas: Proceedings of a</u> <u>Symposium held at the University of Leeds, 22-25 July, 1974.</u> London: Academic Press, pp. 495-509.
- Hayman, D. S. 1970. Endogone spore numbers in soil and vesiculararbuscular mycorrhiza in wheat as influenced by season and soil treatment. <u>Trans. Br. mycol. Soc.</u> 54: 53-63.

- Hepper, C. M., and A. Warner. 1983. Role of organic matter in growth of a vesicular-arbuscular mycorrhizal fungus in soil. <u>Trans. Br. mycol. Soc.</u> 81: 155-156.
- Hetrick, B. A. D., J. F. Leslie, G. T. Wilson and D. G. Kitt. 1988. Physical and topological assessment of effects of a vesicular-arbuscular mycorrhizal fungus on root architecture of big bluestem. <u>New Phytol.</u> 110: 85-96.
- Hoitink, H. A. J., W. Chen, M. I. Trillas-Gay and Y. R. Chung. 1987. Compost for control of plant diseases. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production, Quality, and Use.</u> London: Elsevier Applied Science, pp. 414-419.
- Howard, A. 1947. <u>The Soil and Health: A Study of Organic</u> <u>Agriculture.</u> New York: The Devin-Adair Company.
- Howard, A. 1944. <u>An Agricultural Testament.</u> London: Oxford University Press.
- Hudson, J. C. 1989a. Flyash=Soot=Good news. In: <u>Barbados Sugar</u> <u>Technologists Association: Proceedings of the Seventh Annual</u> <u>Conference, November 22 and 24, 1989.</u> pp. 57-62.
- Hudson, J. C. 1989b. Production of sugar and yields of canetrends in recent times and possible explanations. Paper presented to Barbados Society of Technologists in Agriculture, February, 1989.
- Hudson, J. C. 1970. Meteorology and agriculture in Barbados. Paper prepared for the regional seminar on agricultural meteorology, November 1970.
- Hudson, J. C. and A. Bailey. 1986. Precision filter mud application. Unpublished monograph available from Carib-Agro Industries, Edgehill, St. Thomas, Barbados.

Humbert, R. P. 1968. The Growing of Sugar Cane. London: Elsevier.

- Ishac, Y. Z., M. E. El-Haddad, M. J. Daft, E. M. Ramadan and M. E. El-Demerdash. 1936. Effect of seed inoculation, mycorrhizal infection and organic amendment on wheat growth. Plant and Soil 90: 373-382.
- Janos, D. P. 1987. VA Mycorrhizas in humid tropical ecosystems. In: G. R. Safir, ed. <u>Ecophysiology of VA Mycorrhizal Plants.</u> Boca Raton: CRC Press, Inc., pp. 107-134.

Jodice, R., and P. Nappi. 1987. Microbial aspects of compost application in relation to mycorrhizae and nitrogen-fixing microorganisms. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production</u>, <u>Quality</u>, and Use. London: Elsevier Applied Science, pp. 420-430.

1-1-1

- Johnston, A. 1949. Vesicular-arbuscular mycorrhiza in sea island cotton and other tropical plants. <u>Trop. Agric.</u> 26: 118-121.
- Kapur, M. L., and R. S. Kanwar. 1989. Influence of cane filter cakes and cattle manure on micronutrients content in sugarbeet and their availability in alkaline sandy loam soil. <u>Biol. Wastes</u> 29:233-238.
- Khan, A. G. 1975. Growth effects of VA mycorrhiza on crops in the field. In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. <u>Endomycorrhizas: Proceedings of a Symposium held at the</u> <u>University of Leeds, 22-25 July, 1974.</u> London: Academic Press, pp.419-435.
- Kitt, D. G., B. A. D. Hetrick and G. W. T. Wilson. 1988. Relationship of soil fertility to suppression of the growth response of mycorrhizal big bluestem in non-sterile soil. <u>New Phytol.</u> 109: 473-481.
- Knight, W. G., M. F. Allen, J. J. Jurinak and L. M. Dudley. 1989. Elevated carbon dioxide and solution phosphorus in soil with vesicular-arbuscular mycorrhizal western wheatgrass. <u>Soil</u> <u>Sci. Soc. Amer. J.</u> 53: 1075-1082.
- Koske, R. E., J. C. Sutton and B. R. Sheppard. 1975. Ecology of <u>Endogone</u> in Lake Huron sand dunes. <u>Can. J. Bot.</u> 53: 87-93.
- Kruckelmann, H. W. 1975. Effects of fertilizers, soils, soil tillage, and plant species on the frequency of Endogone chlamydospores and mycorrhizal infection in arable soils. In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. <u>Endomycorrhizas: Proceedings of a Symposium held at the University of Leeds, 22-25 July, 1974.</u> London: Academic Press, pp. 511-525.
- Kruckelmann, H. W. 1973. Die vesikular-arbuskulare Mykorrhiza und ihre Beeinflussung in landwirtschaftlichen Kulturen. Dissertation, Universitat Braunschweig.
- Lanowska, J. 1966. Influence of different sources of nitrogen on the development of mycorrhiza in <u>Pisum sativum</u>. <u>Pamietnik</u> <u>Pulowski.</u> 21: 365-386.
- Lewis, D. G., and J. P. Quirk. 1967. Phosphate diffusion in soil and uptake by plants. <u>Plant and Soil.</u> 26: 454-468.

- Marten, G. G. 1988. Productivity, stability, sustainability, equitability and autonomy as properties for agroecosystem assessment. <u>Agric. Sys.</u> 26: 291-316.
- Mason, S. C., and D. E. Leihner. 1988. Yield and land-use efficiency of a cassava/cowpea intercropping system grown at different phosphorus rates. <u>Field Crops Res.</u> 18: 215-226.
- May, L. H., F. H. Chapman and D. Aspinall. 1965. Quantitative studies of root development. II. The influence of nutrient concentration. <u>Aust. J. Biol. Sci.</u> 18: 25-35.
- Mbagwu, J. S. C. 1989. Effects of organic amendments on some physical properties of a tropical Ultisol. <u>Biol. Wastes</u> 28: 1-13.
- Mbagwu, J. S. C., and A. Piccolo. 1990. Carbon, nitrogen, and phosphorus concentrations in aggregates of organic wasteamended soils. <u>Biol. Wastes</u> 31: 97-111.
- McGonigle, T. P., M. H. Miller, D. G. Evans, G. L. Fairchild and J. A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. <u>New Phytol.</u> 115: 495-501.
- McKeague, J. A. 1978. <u>Manual on Soil Sampling and Methods of</u> <u>Analysis: Second Edition, 1978.</u> Ottawa: Canadian Society of Soil Science.
- Menge, J. A., D. Steirle, D. J. Bagaraj, E. L. V. Johnson and R. T. Leonard. 1973. Phosphorus concentration in plant responsible for inhibition of mycorrhizal infection. <u>New</u> <u>Phytol.</u> 80: 575-578.
- Moberly, P. K., and J. H. Meyer. 1978. Filter cake- A field and glasshouse evaluation. In: <u>Proceedings of The South African</u> <u>Sugar Technologists' Association, 52nd Congress, June 1978.</u> pp. 131-136
- Mosse, B. 1973. Plant growth responses to vesicular-arbuscular mycorrhiza. IV. In soil given additional phosphate. <u>New Phytol.</u> 72: 127-136.
- Mosse, B. 1963. Vesicular-arbuscular mycorrhiza: an extreme form of fungal adaptation. In: P. S. Nutman and B. Mosse, eds. <u>Symbiotic associations: Thirteenth Symposium of the Society</u> <u>for General Microbiology held at The Royal Institution,</u> <u>London, April 1963.</u> Cambridge: Cambridge University Press. pp. 146-170.

- Mosse, B., and G. D. Bowen. 1968. The distribution of <u>Endogone</u> spores in some Australian and New Zealand soils, and in an experimental field soil at Rothamstead. <u>Trans. Br. mycol.</u> Soc. 51: 485-492.
- Mosse, B., D. P. Stribley, and F. LeTacon. 1981. Ecology of mycorrhizae and mycorrhizal fungi. <u>Adv. Microb. Ecol.</u> 5: 137-210.
- Nemec, S. 1987. VA Mycorrhizas in horticultural systems. In: G. R. Safir, ed. <u>Ecophysiology of VA Mycorrhizal Plants.</u> Boca Raton: CRC Press, Inc., pp. 193-211.
- Nicholson, T. H., and C. Johnston. 1979. Mycorrhiza in the Gramineae. III. <u>Glomus fasciculatus</u> as the endophyte of pioneer grasses in a maritime sand dune. <u>Trans. Br. mycol.</u> <u>Soc.</u> 72: 261-268.
- Nkrumah, M., S. M. Griffith and N. Ahmad. 1982-1985. Effect of N¹⁵ fertilizer N and bagasse mulch on N uptake and yield of maize. <u>U.W.I. Faculty of Agriculture Annual Report.</u> 1982-1985: 149.
- Novakova, J. 1987. The clay and compost effects on some characteristics of organic substances in the soil. In: J. Szegi, ed. <u>Proceedings of the Ninth International Conference</u> on Soil Biology and Conservation in the Biosphere. Budapest: Akadémiai Kiado, pp. 541-546.
- Ocampo, J. A., and D. S. Hayman. 1981. Influence of plant interactions on vesicular-arbuscular mycorrhizal infections. II. Crop rotations and the residual effects of non-host plants. <u>New Phytol.</u> 87: 333-343.
- Ofori, F., and W. R. Stern. 1987. Cereal-legume intercropping systems. <u>Adv. Agron.</u> 41: 41-90.
- Owusu-Bennoah, E., and A. Wild. 1979. Autoradiography of the depletion zone of phosphate around onion roots in the presence of vesicular-arbuscular mycorrhiza. <u>New Phytol.</u> 82: 133-140.
- Pairunan, A. K., A. D. Robson and L. K. Abbot. 1980. The effectiveness of vesicular-arbuscular mycorrhizas in increasing growth and phosphorus uptake of subterranean clover from phosphorus sources of different solubilities. <u>New Phytol.</u> 84:327-338.

- Pan, Y. C., K. L. Eow, and S. H. Ling. 1977. The effect of bagasse furnace ash on the growth of plant cane. In: <u>International Society of Sugarcane Technologists:</u> <u>Proceedings XVI Congress. 9-20 Sept. 1977. Sao Paulo,</u> <u>Brazil.</u> Vol. 2, pp. 883-890.
- Patra, D. D., M. S. Sachdev and B. V. Subbiah. 1986. ¹⁵N studies on the transfer of legume-fixed nitrogen to associated cereals in intercropping systems. <u>Biol. Fertil. Soils</u> 2: 165-171.
- Patriquin, D. G. 1982. Nitrogen fixation in sugar cane litter. Biol. Agric. Hort. 1: 39-64.
- Paul, C. L. 1974. effects of filter-press mud on soil physical conditions in a sandy soil. <u>Trop. Agric. (Trinidad)</u> 51: 288-292.
- Pera, A., G. Vallini, I. Sireno, M. L. Bianchin and M. de Bertoldi. 1983. Effect of organic matter on rhizosphere microorganisms and root development of Sorghum plants in two different soils. <u>Plant and Soil</u> 74: 3-18.
- Phillips, J. M., and D. S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesiculararbuscular mycorrhizal fungi for rapid assessment of infection. <u>Trans. Br. mycol. Soc.</u> 55: 158-161.
- Plank, C. O., and D. C. Martens. 1973. Amelioration of soils with fly ash. <u>J. Soil. Wat.</u> 28: 177-179.
- Plenchette, C., et J. C. Fardeau. 1988. Effet du pouvoir fixateur du sol sur le prélèvement de phosphore par les racines et les mycorhizes. <u>C. R. Acad. Sci. Paris</u> 306, Série III: 201-206.
- Plucknett, D. J., and N. J. H. Smith. 1982. Agricultural research and Third World food production. <u>Science</u>. 217: 215-230.
- Prasad, M. 1976a. Response of sugarcane to filter press mud and N, P, and K fertilizers. I. Effect on sugarcane yield and sucrose content. <u>Agron J.</u> 68: 539-543.
- Prasad, M. 1976b. Response of sugarcane to filter press mud and N, P, and K fertilizers. II. Effects on plant composition and soil chemical properties. Agron. J. 68: 543-547.
- Price, N. S., R. W. Rocandori and R. S. Hussey. 1989. Cotton root growth as influenced by phosphorus nutrition and vesiculararbuscular mycorrhizas. <u>New Phytol.</u> 111: 61-66.

- Pugh, L. M., R. W. Rocandori and R. S. Hussey. 1981. factors affecting vesicular-arbuscular mycorrhizal development and growth of cotton. <u>Mycologia</u> 73: 869-880.
- Reed, H. S., and T. Frémont. 1935. Factors that influence the formation and development of mycorrhizal associations in citrus roots. <u>Phytopathol.</u> 25: 645-647.
- Reeve, N. G., and M. E. Sumner. 1970. Effects of aluminum toxicity and phosphorus fixation on crop growth on Oxisols in Natal. <u>Soil Sci. Soc. Amer. Proc.</u> 34: 263-267.
- Robinson, J. B. D. 1951. A brief review of sugar-cane manuring in Barbados. Proc. Brit. W. Ind. Sug. Tech. 1951: 73-77.
- Rutili, A., M. Civilini, B. Citterio, S. Frassinetti and M. De Bertoldi. 1987. Microbial variations in compost amended soils. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production, Quality, and Use.</u> London: Elsevier Applied Science, pp. 615-632.
- Saint, G. 1932. A discussion of the results of manurial trials carried out on sugar-cane in Barbados, 1928-1932. <u>Agric. J.</u> <u>Barbados.</u> 1: 1-23.
- Salem, N., M. Verloo and M. De Boodt. 1987. Organic waste as soil amendments for the redemption of Egyptian sandy soils. I. Effects of different combinations of organic wastes. In: M. De Bertoldi, M. P. Ferranti, P. L'Hermite and F. Zucchoni, eds. <u>Compost: Production, Quality, and Use.</u> London: Elsevier Applied Science, pp. 453-463.
- Sanchez, P. A., and J. R. Benites. 1987. Low-input cropping for acid soils of the humid tropics. <u>Science</u>. 238: 1521-1527.
- Sanders, F. E., and P. B. Tinker. 1973. Phosphate flow into mycorrhizal roots. <u>Pestic. Sci.</u> 4: 385-395.
- Simmons, G. L., and P. E. Pope. 1988. Influence of soil water potential and mycorrhizal colonization on root growth of yellow- poplar and sweet gum seedlings grown in compacted soil. <u>Can. J. For. Res.</u> 18: 1392-1396.
- Simmons, G. L., and P. E. Pope. 1987. Influence of soil compaction and vesicular-arbuscular mycorrhizae on root growth of yellcw poplar and sweet gum seedlings. <u>Can. J.</u> <u>For. Res.</u> 17: 970-975.
- Singh, J. P., R. E. Karamanos and J. W. B. Stewart. 1986. Phosphorus-induced zinc deficiency in wheat on residual phosphorus plots. <u>Agron. J.</u> 78: 668-675.

- Slankis, V. 1974. Soil factors influencing formation of mycorrhizae. <u>Ann. Rev. Phytopathol.</u> 12: 437-457.
- Smith, S. E. 1980. Mycorrhizas of autotrophic higher plants. Biol. Rev. Cambridge Philos. Soc. 55: 475-510.
- St. John, T. V. 1980. Root size, root hairs, and mycorrhizal infection: A re-examination of Baylis's hypothesis with tropical trees. <u>New Phytol.</u> 84: 483-487.
- St. John, T. V., D. C. Coleman and C. P. P. Reid. 1983a. Association of vesicular-arbuscular mycorrhizal hyphae with soil organic particles. <u>Ecology</u> 64: 957-959.
- St. John, T. V., D. C. Coleman and C. P. P. Reid. 1983b. Growth and distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. <u>Plant and Soil</u> 71: 487-493.
- Stinner, B. R., and G. J. House. 1989. The search for sustainable agroecosystems. J. Soil Wat. 44: 111-116.
- Stribley, D. P., and D. J. Read. 1980. The biology of mycorrhiza in the Ericaceae. VII. The relationship between mycorrhizal infection and the capacity to utilize simple and complex organic nitrogen sources. New Phytol. 86: 365-371.
- Strzemska, J. 1975. Mycorrhiza in farm crops grown in monoculture.In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. Endomycorrhizas: Proceedings of a Symposium held at the University of Leeds, 22-25 July, 1974. London: Academic Press, pp. 527-543.
- Tennant, D. 1975. A test of a modified line intersect method of estimating root length. <u>J. Ecol.</u> 63: 995-1001.
- Tinker, P. B. 1984. The role of microorganisms in mediating and facilitating the uptake of plant nutrients from soil. <u>Plant</u> and <u>Soil</u> 76: 77-91.
- Tinker, P. B. 1975. Soil chemistry of phosphorus and mycorrhizal effects on plant growth. In: F. E. Sanders, B. Mosse and P. B. Tinker, eds. <u>Endomycorrhizas: Proceedings of a Symposium held at the University of Leeds, 22-25 July, 1974.</u> London: Academic Press, pp. 353-371.
- Vernon, K. C., and D. M. Carroll. 1965. <u>Soil and Land-Use Surveys</u> <u>No. 18: Barbados.</u> Trinidad: The Imperial College of Tropical Agriculture.

Wahua, T A T. 1983. Nutrient uptake by intercropped maize and cowpeas and the concept of Nutrient Supplementation Index (NSI). <u>Expl. Agric.</u> 19: 263-275.

- Walker, D. I. T. 1986. Filter mud: How to obtain the most benefit from its application. <u>ARU Research Bulletin:</u> Number 44.
- Warner, A. 1984. Colonization of organic matter by vesiculararbuscular mycorrhizal fungi. <u>Trans. Br. mycol. Soc.</u> 82: 352-354.
- Warner, A., and B. Mosse. 1982. Factors affecting the spread of vesicular-arbuscular mycorrhizal fungi in soil. I. Root density. <u>New Phytol.</u> 90: 529-536.
- Willey, R. W. 1979. Intercropping: Its importance and research needs. Part 1. Competition and yield advantages. <u>Field Crop</u> <u>Abs.</u> 32: 1-10.
- Yates, R. A. 1964. Yield depression due to phosphate fertilizer in sugar-cane. <u>Aust. J. Agric. Res.</u> 15: 537-547.

APPENDIX ONE:

The effect of a maize intercrop on mycorrhizal infection of sugarcane

Introduction:

Intercropping, the practice of planting more than one crop in a field at the same time, often results in more efficient use of land than growing the component crops monoculturally (Willey, 1979; Ofori and Stern, 1987). Such yield advantage may result from a more complete and efficient use of growth resources: light, water, and soil nutrients. Intercropped species may be, at least partially, complementary rather than competitive in their resource use patterns: in time, space, or some qualitative Alternatively, there may be symbiotic and other direct manner. interactions of plant combinations, such as the transfer or leakage of fixed nitrogen from legumes to non-legumes (Bandyopadhyay and De, 1986; Patra et al., 1986).

One direct interaction of coexisting crops occurs through microflora effects. It has been postulated that mycorrhizal links effect phosphorus and nitrogen transfer between intercrops. Crop rotation regimes (Ocampo and Hayman, 1981; Black and Tinker, 1979), have been shown to alter the percent infection of a plant species, both positively and negatively, through influences on soil spore populations.

Interplanting one crop with another, strongly mycorrhizal, crop may result in increased percent infection through cross-

inoculation. This could be particularly evident in plants combinations with different resource demands in time, if they also develop mycorrhizae at different times. Due to increased plant density and phosphorus competition of some mixtures (Mason and Leihner, 1988; Chang and Shibles, 1985; Wahua, 1983) intercropping may accelerate soil phosphorus depletion, thereby stimulating the mycorrhizal association. Simple increases in root density can increase VAM spread (Abbott et al., 1984; Warner and Mosse, 1982).

The following experiment was undertaken to determine if a maize intercrop affected the mycorrhizal status of sugarcane.

Methcds:

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An intercrop was examined at Todds plantation where a double row of maize (M) had been planted in alternate interrows of plant cane (C), in a CCMMCCMM arrangement. Cane rows were 1.75 m apart, paired maize rows 0.45 m from each other and 0.65 m from the nearest cane row. Banks had been split.

Root samples were taken at two times: two weeks after the maize had been harvested (11/89), and three months later. For the initial samples, the auger used for 1989 Edgecumbe sampling was employed to take a set of three cores from an adjacent CCMM group at six random sites. Each set consisted of (1) a core 15 cm from the cane stem in the CC interrow, (2) a core 15 cm from the cane stem in the CM interrow, and (3) a core 15 cm from the maize stem in the MM interrow. These were meant to represent

cane roots unaffected by maize, cane roots in contact with maize, and maize roots, respectively. As well, a set of five cores were taken from an adjacent monocrop cane field with unsplit banks. Root samples were processed for weight, length, and mycorrhizal infection as previously described for compost samples. Percentage infection was assessed using the gridline intersect method (Giovannetti and Mosse, 1980), at 50X magnification.

Three months after the initial samples, roots in the CM and CC interrows, and from the adjacent field, were sampled at 0-30 cm from cane stems to 10 cm depth using a trowel. Ten CCM sets and ten monocrop cane plants were sampled. Due to the completely senescent state of the maize at this time, their roots could be easily distinguished and discarded. Samples therefore contained only cane roots, as opposed to the earlier CM cores which may have contained both. These samples were stained as previously described and infection assessed using the method of McGonigle et al. (1990).

Results and Discussion:

A MANOVA of root weight, root length, SRL, THC and ACC for the initial samples showed significant treatment effects (Pillai trace p=0.008) for weight (p=0.014) and ACC (p=0.002). However these were almost completely due to high infection and low root weight of the MM treatment. Rooting of monocrop cane was also less than intercrop cane, but this could have been due to the fact that banks were not split. Contrasts of ACC for CM versus
CC (p=0.091) and CM versus CC + monocrop cane (p=0.125), were not significant.

There was little evidence for the hypothesis that cane roots utilizing the same soil volume as heavily-infected maize roots supported unusually high infection. In fact, due to the uncertainty factor of the assessment method used here, it is unsure even if the fungus observed was mycorrhizal. It seems likely from the senescent state of the maize that at least a portion of the infection was decomposer fungi. Any trend towards higher infection in CM over CC roots could also be accounted for by the presence of some maize roots in CM samples.

The later sampling phase overcame these methodological problems. However, the MANOVA of THC, VC, CC, AC, ACC, and HC showed no significant differences in infection of sugarcane roots adjacent to maize plants as compared to roots not adjacent to maize, or cane roots in the monocrop field (Pillai trace p=0.655).

There could have been some effect on mycorrhizal structures undetected by the initial, inexact method of assessment which did not remain after the maize began to senesce in earnest. From the evidence, however, it appears that maize roots truly did not affect mycorrhizal status of cane, due to strain specificity, lower affinity of cane for mycorrhiza, or some other factors.

APPENDIX TWO:

List of abbreviations and acronyms

AC Arbuscular colonization

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- ACC Arbuscule/coil colonization
- ACRL Arbuscule/coil infected root length
- ANOVA Analysis of Variance
- ARU Agronomy Research Unit of the Barbados Sugar Industry Limited
- BSIL Barbados Sugar Industry Limited
- CC Coil colonization
- FYM Farm yard manure
- HC Hyphal (total mycorrhizal) colonization
- IRL Infected root length
- MANOVA Multivariate Analysis of Variance
- SE Standard error
- SRL Standard rooting length
- THC Transverse (intercellular) hyphal colonization
- TSP Triple superphosphate
- VAM Vesicular-arbuscular mycorrhizae
- VC Vesicular colonization