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Biologically regulated nutrient supply systems: compost and arbuscular mycorrhizas - a review

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Running title: Compost and arbuscular mycorrhizas

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Abstract:

To achieve global food security, we will need to produce more food, and do so in an environmentally sustainable manner. Inorganic fertilizers have be instrumental in increasing food production, but with some fertilizers becoming increasing scarce and expensive, we also need to consider other options for providing agricultural plants with nutrients. To this end, there has been increased interest in the potential to make better use of the nutrients tied up in organic matter; composts are an example of this, and are the focus of this review. Plant nutrient acquisition can be enhanced through the formation of arbuscular mycorrhizas (AM). The purpose of this review is to explore interactions between compost and AM, with an emphasis on the impacts of compost addition and formation and functioning of AM. Based on available literature it is clear that the application of compost either has a positive or neutral effect on the formation of the symbiosis, and that dual application of compost and arbuscular mycorrhizal fungi (AMF) provides clear benefits to plants in terms of growth and nutrition. There is also emerging evidence that dual application also provides benefits in terms of soil structure. Taken together, the conclusion of this review is that that biologically regulated nutrient supply systems based on compost and AM are compatible.

Key words: Arbuscular mycorrhizas (AM), Biologically Regulated Nutrient Supply Systems, Compost, Organic Amendments, Sustainability.

Introduction and Scope of Review

Achieving agricultural and environmental sustainability is a global imperative. It has been projected that we will need to double food production by 2050 in order to achieve global food security (United Nations, 2013). A significant proportion of the increase in global food production since the mid-20th Century can be attributed to the use of inorganic fertilizers; however, these same fertilizers are projected to become increasingly scarce in the coming decades (Cordell et al., 2009). Further, many of the World's farmers, especially those in the developing world where much of the projected increase in the human population is to occur, do not have ready access to inorganic fertilizers (Burns et al., 2010, Cardoso and Kuyper, 2006). Thus, there has been considerable emphasis placed on the identification and utilization of alternative nutrient sources, such as organic amendments, to support agricultural production and achieve food security (Jackson et al., 2008, Conyers and Moody, 2009, Hargreaves et al., 2008, Nelson and Janke, 2007, Quilty and Cattle, 2011).

Many different types of organic amendments are used to supply nutrients to plants (e.g. see Quilty and Cattle, 2011, Nelson and Janke, 2007). These include cover crop residues and green manures, raw, composted and pyrolysed biomass, humic and fulvic acid containing preparations, vermicasts, and seaweed emulsions and extracts, to name but a few. While inorganic fertilizers are used in much of the World's agriculture, for most of its history, agriculture has primarily relied on organic amendments and soil biological processes for the provisioning of nutrients to plants (Quilty and Cattle, 2011). Indeed it can be argued that most of the World's farmers - that is, subsistence farmers - rely on biologically regulated nutrient supply systems to support production. Similarly organic farming systems provide nutrients to plants from organic sources (Watson et al., 2002, Nelson and Janke, 2007, Cavagnaro et al., 2006). There is also an emerging trend towards hybrid farming systems where both organic and inorganic sources of nutrients are being used to support production (Placea et al., 2003).

Many organic amendments are produced using on- or off-farm waste streams, such as urban/municipal green waste, animal manure, and others (Quilty and Cattle, 2011). With increasing resource scarcity, the potential to recover nutrients from organic waste streams that may otherwise be wasted (Hargreaves et al., 2008), provides benefits beyond agricultural production alone. However, whereas inorganic fertilizers (generally) provide a predictable supply of nutrients to plants, organic amendments are less predictable in terms of nutrient supply. This is because organic amendments typically contain nutrients in many different forms (Hargreaves et al., 2008), and these nutrients need to be mineralized before they are accessible to (most) plants (Ng et al., 2014b, Ng et al., 2014a). This lack of predictability complicates efforts seeking to tailor application rates and timing to meet crop demands. Indeed it is likely that a lack of predictability may result in over application, which is both expensive, and potentially environmentally damaging. Thus, for organic amendments to become part of mainstream agriculture they need to be reliable, and this depends on knowledge of the mechanisms that underpin their behaviour in the soil.

Of the many organic amendments currently used in agriculture, composts are one of the most widely used, and are the focus of this review. They are produced via biologically-mediated oxidative processes that yield humified organic matter (Hargreaves et al., 2008, Quilty and Cattle, 2011, Zmora-Nahum et al., 2007). Feedstocks for composts include, but are not limited to, urban and municipal waste, greenwaste, farmyard manure and crop residues. Composts are reported to provide many benefits, including the provisioning of nutrients to plants and other soil biota over both the short and long term, addition of organic matter to the soil, release of humic and fulvic acids, improvements in soil structure and cation exchange capacity, and disease suppression (see Quilty and Cattle, 2011, for recent review). It is for these reasons that composts have been, and will continue to be, an important part of global agriculture.

If modern agriculture is to increasingly rely upon biologically regulated nutrient supply systems, then we need to consider not only the biological processes that drive the cycling and transformations of organic nutrient sources in the soil, but also the soil biological processes that are involved in plant nutrient acquisition. To this end, arbuscular mycorrhizas (AM) - associations formed between most terrestrial plant species and arbuscular mycorrhizal fungi (AMF) - can greatly enhance the capacity of plants to acquire nutrients from the soil (Smith and Read, 2008). It is well established how the formation and functioning of AM is affected by the addition of inorganic nutrients, especially P, but also N and Zn, to the soil (see Cavagnaro, 2008, Smith and Smith, 2011, Veresoglou et al., 2012, for recent review). In contrast, the response of AM to the addition of organic amendments to the soil has not been widely explored. If we are to move towards an agricultural paradigm underpinned by biologically regulated nutrient supply systems, then we need to consider the role of AM in plant nutrient acquisition, and how it is impacted upon by the addition of organic amendments to the soil.

Whereas the relationship between AM and inorganic nutrient supply has been widely reviewed (Cavagnaro, 2008, Harrison, 1999, Smith and Read, 2008, Smith and Smith, 2011, Veresoglou et al., 2012), the interaction between AM on organic nutrient sources of nutrients has not. Therefore, here I present a review of the impact of compost addition on the formation and functioning of AM. Following a brief discussion of AM, this review focuses its attention on:

i. Compost effects on the formation of AM;
ii. Compost effects on the production of propagules of AMF;
iii. Interactive effects of compost and AMF on plant growth and nutrition; and
iv. Interactive effects of compost and AMF on soil properties.

As is always the case in writing a review, it is not possible to include all published work. However, in an effort to identify broader patterns in the literature, I have produced a tally of responses of AM, in terms of formation and functioning, to compost addition. These responses are then further explored through reference to specific studies. Finally, the review is concluded with a brief discussion of knowledge gaps, with a view to stimulating further work in this area.

Arbuscular mycorrhizas: a brief overview

Arbuscular mycorrhizas play an important role in the plant uptake of especially inorganic P, but also N, Zn, Cu, Fe and other nutrients (Bürkert and Robson, 1994, Frey and Schuepp, 1993, Marschner and Dell, 1994, Cavagnaro et al., 2010, Adesemoye and Kloepper, 2009, Veresoglou et al., 2012). In return, the fungi benefit from a supply of C from the plant; plants can allocate a substantial proportion of their assimilated C, between 4 and 20%, to AMF (Jakobsen and Rosendahl, 1990, Mortimer et al., 2005, Cavagnaro et al., 2008).

While most studies have focused on the capacity of AMF to acquire nutrients from inorganic sources, there also is some evidence to suggest that AM may be able to acquire N from organic sources (Hodge et al., 2001, Hodge and Fitter, 2010, Veresoglou et al., 2012). However, it has been suggested that AMF are not directly involved in N release from organic matter, but rather they acquire mineralized inorganic N (see Smith and Smith, 2011, for recent review). With organic N being a major component of compost, the potential for AMF to acquire N, irrespective of whether it is in its organic or mineral forms, may be important (Veresoglou et al., 2012). This is especially true with respect to systems where nutrients are applied in organic forms such as composts.

The chief mechanisms by which AM enhance plant nutrient acquisition is via their capacity to acquire nutrients from beyond rhizosphere nutrient depletion zones, and by accessing nutrients from microsites not directly accessible to roots (Drew et al., 2003, Jakobsen et al., 1992). In doing so, AM not only increase plant nutrient acquisition, but in some cases, they can serve as the principal or sole pathway by which plants acquire nutrients (Smith et al., 2004). Hyphal ramification through the soil can also result in improvements in soil structure, via enmeshment and entanglement mechanisms and the exudation of polysaccharides that help to bind soil particles together (Rillig and Mummey, 2006).

The formation of AM is strongly affected by edaphic conditions and soil management. For example, increased supply of inorganic nutrients, especially P, can result in decreased levels of AM colonization (Baon et al., 1992, Harrison, 1999, Oliver et al., 1983). The same is also true for N and other nutrients also (Treseder, 2004, Watts-Williams and Cavagnaro, 2012). Whether or not levels of AM colonization are affected, be it positively or negatively, by the supply of organic forms of nutrients, remains to be seen. The formation of AM can also be adversely affected via management practices that disturb AMF, such as tillage and the use of fungicides and other pesticides (Miller and Jackson, 1998, Cavagnaro and Martin, 2011). These factors may be relevant depending on the mode of compost application and incorporation.

Taken together, it is clear that AM play an important role in plant nutrition, especially when nutrients are applied in inorganic forms. Whether or not the same is true where nutrients are supplied as organic amendments remains to be seen. If, however, we are to see an increased reliance on biologically regulated nutrient supply systems, this issue needs to be explored. This includes consideration of the effect of compost, and indeed other organic amendments, on the formation and functioning of AM, and so, this is the focus of the remainder of this review.

Review – methods

In order to identify potential impacts of compost on the formation of functioning of AM a search of ISI web of knowledge was undertaken using the search terms ‘compost’ AND ‘arbuscular mycorrhizas’ OR ‘mycorrhizae’. Publications identified in this search were used to gain insights into the issues, as well as to identify some general patterns in responses of AM to composts. Very few (in fact almost none), of the studies identified provided data on compost maturity, and so, materials applied to the soil were considered compost if so referred to in the papers cited. Further, in many papers relatively little detail was given on the materials used to produce composts, and so it was not possible to separate out different compost types in this review.

Given the tremendous variation in the types and rates of composts added to the soil, and the relatively small number of publications (see below), it was not possible to perform a complete meta-ananlysis with sufficient confidence. Therefore, a more conservative approach was taken in which patterns in responses of AM to compost were identified by taking a simply tally of AM responses to compost addition, be them positive, negative or neutral. Specifically, a response, be it in terms of AM colonization of roots, plant growth and plant nutrition, was deemed to have occurred where a significant increase or decrease following compost addition was observed. This was based on either using the statistics provided in the paper, or where statistics were not included or did not allow comparison of treatments, a difference was deemed to exist where means differed by one or more standard error. In some instances a single paper compared multiple compost types, soil types, plant species, etc., and so contributed more than one data pair. Papers were omitted where statistics or a measure of error were not included, where data presented were identical to those in a separate publication (i.e. the same data were included only once in the tallies presented here), or where the control and compost addition treatment differed in ways aside from compost addition (e.g. addition of other microorganisms or materials, or comparisons of whole farming systems). The publications from which tally data were ultimately derived are cited herein

(Adewole and Ilesanmi, 2011, Alguacil et al., 2006, Alguacil et al., 2004, Bilalis and Karamanos, 2010, Caravaca et al., 2006, Caravaca et al., 2005, Caravaca et al., 2002b, Caravaca et al., 2003b, Caravaca et al., 2003c, Caravaca et al., 2002c, Copetta et al., 2011, Douds and Reider, 2003, Duong et al., 2012, Gryndler et al., 2008, Jacquot-Plumey et al., 2003, Jacquot-Plumey et al., 2001, Kaushish et al., 2011, Krey et al., 2011, Krey et al., 2013, Linderman and Davis, 2001, Marosz, 2012, Noyd et al., 1996, Osorio et al., 2002, Palenzuela et al., 2002, Puschel et al., 2008, Roldan et al., 2008, Sainz et al., 1998, Simon et al., 2006, Tanwar et al., 2013, Tarkalson et al., 1998, Totola and Borges, 2000, Caravaca et al., 2003a, Caravaca et al., 2002a, Viti et al., 2010, Wu et al., 2011, Celik, 2009, Celik et al., 2004, Daynes et al., 2013, Ortas et al., 2013, Roldan et al., 2006, Celik et al., 2010, El-Din et al., 2000, Johnson, 1998, Marques et al., 2008, Mendes Filho et al., 2010, Vaidya et al., 2008, Valarini et al., 2009).

Compost effects on the formation of AM

The addition of inorganic nutrients, especially P, generally has a negative effect on mycorrhizal colonization of roots (see above). With a move towards greater reliance on organic amendments, such as composts, an important question that remains is whether or not compost addition will have a negative, positive or neutral effect on AM colonization. A number of studies have investigated this question, by assessing changes in colonization in responses to a range of different compost types, plant and fungal species, and rates of compost application (Copetta et al., 2011, Tanwar et al., 2013, Marosz, 2012, Duong et al., 2012, Valarini et al., 2009). In an attempt to identify larger scale patterns, a survey of the literature was undertaken. The direction of change, be it an increase, decrease or no change in colonization, in response to compost addition was recorded for studies identified in this review of the literature. This information was then used to answer two questions in relation to compost and AM.

Question 1a. Does the application of compost alone have an effect on AM colonization of roots?

A total of 104 data pairs from 36 published papers were identified in which this question was addressed. These studies found that compost most often had a positive or neutral effect on AM colonization (Figure 1a); possible reasons for this are considered below. In those studies where compost addition had a negative effect on AM colonization, there was no clear indication as to the cause; that is, reductions in colonization were not associated with specific types of compost, plant species or other readily apparent factors.

[NOTE: INSERT FIGURE 1 HERE. CAPTION: **Figure 1** Change in mycorrhizal colonization of roots (per cent root length colonized) following the addition of **(a)** compost, compared to where neither compost nor AMF were added, and **(b)** compost and AMF were added, compared to where only AMF were added.]

Question 1b. Does the application of compost along with AMF have an effect on AM colonization compared to the addition of AMF alone?

A total of 53 data pairs, originating from 21 publications, were identified in which this question was asked. Overall, the dual application of compost and AMF had a neutral or positive effect on levels of AM colonization, compared to where only AMF were added to the soil (Figure 1b). This suggests that, on balance, the addition of compost is compatible with the addition of AMF; however, the addition of AMF together with compost did not greatly enhance the capacity of AMF to colonize roots. This is in direct contrast to a situation where AMF are added to the soil together with inorganic nutrients, which would, under high levels of nutrient supply, generally result in a reduction in colonization relative to the addition of AMF alone (Baon et al., 1992, Harrison, 1999, Oliver et al., 1983).

Where compost and AMF were added together, in only one third of cases were levels of AM colonization lower compared to where AMF were added alone (Figure 1b). However, in all of those cases, the level of colonization (where AMF and compost were added together) was still higher than that where neither AMF nor compost were added. Thus, it appears that at worst, the addition of compost together with AMF will still result in higher levels of colonization than if neither are added to the soil. This finding is important, as it suggests that both AMF and compost can be added simultaneously, which has advantages from an agronomic standpoint, and is in contrast to the supply of some nutrients (especially P) in inorganic forms.

There are a number of possible reasons as to why the addition of compost may increase AM colonization of roots. Composts applied to the soil may contain propagules of AMF. However, given that a feature of the composting process is an increase in temperature (Fernandes et al., 1994), which can eliminate or reduce the levels of microbes present in the soil (Hargreaves et al., 2008), this is unlikely to be a major factor. This is supported by one study in which plants grown in only compost had very low levels of AM colonization (0.5%+/-0.5 root length colonized) compared to unamended soils or soils where lower rates of compost were added and colonization levels were higher (Copetta et al., 2011).

Nutrient supply can also affect colonization of roots by AMF. Nutrient addition to the soil generally results in a decrease in AM colonization, whereas, in some instances it can result in an increase colonization. For example, in one study colonization was inhibited at low levels of soil P, with small additions of P colonization was slightly increased (Bolan et al., 1984). A similar response has been found following Zn addition to the soil too (Lee and George, 2005, Zhu et al., 2001). Further, the interactive effects of nutrient supply on AM colonization cannot be discounted; for example colonization can be stimulated by low N availability where soil P availability is high (Blanke et al., 2005). Further, the 'slow-release' nutrients from composts may establish a situation where available levels of nutrients are not so high as to reduce AM colonization, but are high enough to stimulate, colonization of roots by AMF; this, however, is speculative. Nevertheless, that the addition of compost does not have a negative impact on AM colonization might be expected given that this is similar to natural systems where nutrient inputs are largely organic in nature, and reliant upon the decomposition of organic matter. Irrespective of the mechanisms involved, it is clear that adding compost to the soil alone is in most cases compatible with the maintenance, or promotion, of the formation of AM.

To further explore the effects of compost on the formation of AM, selected case studies will now be considered. The effect of the application of six different types of compost on the formation of AM by wheat was investigated by Duong *et al*. (2012). It was found that five out of the six composts applied resulted in an increase in AM colonization of up to 50%. Interestingly, the level of colonization was negatively correlated with the plant available P in the compost, which is consistent with effects of inorganic P supply on AM colonization (Baon et al., 1992, Harrison, 1999, Oliver et al., 1983). However, in this case the negative correlation between colonization and P was due to a decrease in the extent to which AM colonization was stimulated by compost addition, rather than an overall reduction in colonization.

A number of studies have investigated the effect of increasing rates of compost supply on AM colonization. Results have been variable, with increasing levels of compost application resulting in increasing (Tanwar et al., 2013) and decreasing (Copetta et al., 2011) levels of colonization. Interestingly, the response of different plant species to the same compost can differ. For example Valarini et al. (2009) reported a general increase in colonization of Wheat and Beans, but no change in colonization of a mixture of grassland species, in response to increasing rates of compost. Given the limited number of studies available that apply the same compost at different rates, and the large variation in the rates of compost applied among studies, it would be premature to draw firm conclusions on the impact rates of compost application on AM at this stage. Such studies will be important in optimizing compost application rates, both from the point of view of maximizing levels of AM colonization, as well as from economic and agronomic standpoints.

Plants differ in their capacity to form, and their reliance upon, AM. To this end, it is no surprise that the application of the same compost on different plant species yield variable results. For example, when supplied with a compost derived from the organic fraction of municipal waste together with AMF

(Palenzuela et al., 2002), the change in colonization varied considerably between plant species: colonization of *Pistacia lentiscus* increased from 7% to 47%; *Retama sphaerocarpa* increased from 13 to 37%; *Olea europeae* increased from 15 to 65%; and *Rhamnus lycodies* increased from 1 to 38%. Similarly, when greenwaste compost was applied to seven different species of woody shrubs (Marosz, 2012), colonization was increased, decreased and remained the same, in two, one and four of the species, respectively. These examples serve to highlight the need to carefully match composts to plant species, particularly where the aim is to increase levels of AM colonization; the same is also true where the aim is to improve plant growth, or other factors (see below). A similar result, in terms of growth responses of plants with the the addition of humic substances to the soil, has been reported (Rose et al., 2014).

The impact of compost addition on the formation of AM can be affected by the identity of the fungi (Alguacil et al., 2004, Osorio et al., 2002, Totola and Borges, 2000). For example, Alguacil et al. (2004) report an increase in colonization of roots by (the then named) *Glomus intraradicies* (now named *Rhizophagus irregularis*), *G. deserticola* and *G. mosseae*. In contrast, Osorio et al. (2002) report no change in colonization of roots by *Entrophospora colombiana*, or a mixture of 'native' and foreign' AMF following compost application. Similarly, Totola and Borges (2000) report no change in colonization of roots by *Aculospora scrobiculata* and *Gigaspora margarita* when they were added to the soil, but a decrease when *G. etunicatum* was added. Given the tremendous functional diversity among AMF (Drew et al., 2003, Smith et al., 2004, Cavagnaro et al., 2005), this response in not unexpected, and again warrants further investigation, especially in the context of dual application of AMF and compost, or the production and delivery of AMF inoculants in compost (see below).

AM colonization and compost – conclusions

Based on the publications considered here, it is concluded that the addition of compost to the soil is compatible with maintaining or enhancing levels of colonization of roots by AMF(measured as % colonization). This finding is important as it demonstrates that nutrient supply systems based on compost, in most cases, do not adversely affect a key group of soil organisms involved in plant nutrient acquisition. The mechanisms that underpin the increase, and in some cases the decrease, in levels of AM colonization following compost addition remain to be elucidated. It will also be important to taken into consideration impacts on root length as well as precent colonization of roots of AMF. For example, a small decrease (on no change) in precent colonization of roots by AMF can be accompanied by a large increase in root biomass with compost addition. Consequently, a decrease in precent colonization may actually mask positive effects of compost on the formation of AM being overlooked. Be that as it may, the vast majority of studies on AM report precent colonization data rather than data on root length colonized; this is a point that should be considered in such studies. Further investigation will also be required if we are to tailor compost application to maximize the formation of AM. This will be especially important in helping to avoid those situations, albeit rare, where compost addition results in a decrease in levels of colonization. It will also help avoid excess compost application, which is both costly, and potentially environmentally damaging.

Compost effects on propagules and extra-radical growth of AMF

Spores are important propagules of AMF. In addition to providing a source of inoculum, they are also important for dispersal of AMF, and serve as resting structures that can persist in the soil for long periods of time (Smith and Read, 2008). Given that compost addition can affect the formation of AM (see above), and that AMF need to colonize plant roots to complete their life cycle, it follows that the addition of compost to the soil may have an effect on spore densities in the soil. In an attempt to address this issue, the following question was explored.

Question 2. Does the application of compost alone have an effect on the abundance of spores of AMF in the soil?

A total of 22 data pairs, originating from five publications, addressing this question were identified. In nearly three quarters of cases the addition of compost to the soil had a positive effect on the abundance of AMF spores in the soil at the end of a plant growth cycle (Table 1). In all other cases there was no change.

One possible explanation for an increase in spores of AMF with compost addition is that the composts applied contained spores; however, in no studies was this directly investigated. The addition of spores to the soil with compost may also explain higher levels of colonization in treatments receiving compost. Given that one of the chief aims of composting is to reduce the abundance of microbes, due to the generation of heat during the composting process, this seems unlikely. For example, a mature compost will typically reach temperatures of 60-65°C (Fernandes et al., 1994). While treatment of soil at this temperature can dramatically reduce the inoculum potential of soils (Endlweber and Scheu, 2006), it does not necessarily eliminate (especially) spores of AMF. It is also important to note this explanation only holds if the composts achieved such temperatures during production.

Another possible explanation for an increase in spore abundance is increased levels of colonization (see above) in treatments receiving compost. However, whereas in one of the papers where there was an increase in spores there was an increase in AM colonization of roots (Noyd et al., 1996), in another two AM colonization was the same (Viti et al., 2010, Palenzuela et al., 2002), and in the remaining two studies corresponding spore and colonization data were not reported (Celik, 2009, Vaidya et al., 2008). Thus, it is to soon to attribute changes in spore abundance to increased levels of colonization. Another possible explanation is that soil nutrient supply can also affect the abundance of AM propagules (Treseder, 2004, Treseder and Allen, 2002). For example, in a systems comparison (NPK addition versus compost addition) Vaidya et al. (2008) reported a trend towards higher spore densities in treatments receiving compost than those receiving inorganic P. Again, more studies investigating these links are required.

Some studies have investigated the impacts of compost addition, not only on the abundance of spores of AMF, but also the composition of the spore community. For example, Vaidya *et al.* (2008) found that the relative abundance of spores of different species of AMF differed depending on whether soils were amended with compost or inorganic P. Given that AMF differ substantially in their ability to acquire and supply nutrients to plants (Drew et al., 2003, Smith et al., 2004, Cavagnaro et al., 2005), it follows that they may also be differently affected by nutrient supply.

Interestingly, only one study was found where the effect of adding compost and AM together was compared to the addition of AMF alone (Palenzuela et al., 2002). In this case it was found that spore densities were the same in both treatments. Further such studies would be useful in determining whether or not the application of AMF together with compost has a synergistic, additive, neutral or negative impact on AMF spore densities. This is also relevant to the optimization of AMF inoculum production and application. To this end, the effect of adding compost to media used to produce AMF inoculum has been explored (Douds, 2009, Douds et al., 2010, e.g. Douds et al., 2006, Douds et al., 2008). For example, Douds et al. (2006) found that compost and vermiculite mixtures contained more propagules of AMF than soil-based mixtures, and that the resulting inoculum was suitable for use in vegetable production systems. This again, is an area suitable for further investigation, and is of considerable practical importance.

Two publications were identified in which effects of compost on the extraradical growth of AMF (measured as hyphal length density) into the soil was reported (Palenzuela et al., 2002, Valarini et al., 2009). Valarini et al. (2009) found that with the addition of compost, the growth of hyphae into the surrounding medium both increased and decreased, depending upon the plant species. In contrast, Palenzuela et al. (2002) found a consistent increase in extraradical growth following compost supply with four different plant species. Again, further studies will be required before general patterns can be identified.

A number of studies have investigated the effect of compost addition on the concentration of various lipids that have been suggested as being AMF specific biomarkers for AMF in soils (Bastida et al., 2008, Elfstrand et al., 2007, Labidi et al., 2007, Garcia et al., 2007). While these studies mostly show an increase in these biomarkers, there is increasing caution around the use of specific lipids as biomarkers for specific groups of organisms (Frostegård et al., 2011), and so such results should be considered in this light.

While there are few studies investigating the impact of compost of the extraradical growth of AMF, a positive effect could be very significant. The hyphae of AMF provide plants with a well-distributed and extensive absorbing system in soil that enhances their likelihood of encountering nutrient rich microsites not available to the roots alone. Further, hyphae of AMF can rapidly proliferate in nutrient patches allowing them to acquire nutrients rapidly (Cavagnaro et al., 2005, Tibbett, 2000, Facelli and Facelli, 2002). Thus, colonization of nutrient patches by the external hyphae of AMF would allow them to acquire mineral nutrients as the organic constituents of the compost are mineralized (Smith and Smith, 2011). In addition to improving plant nutrition, this could also reduce the risk of nutrient loss via leaching (Asghari and Cavagnaro, 2011, Asghari and Cavagnaro, 2012, Asghari et al., 2005, van der Heijden, 2010). Thus, investigation into the response of the external hyphae of AMF to compost addition should be of high priority.

Compost effects on propagules and extra-radical growth of AMF– conclusions.

While there are relatively few studies that have investigated the effect of compost addition on the production of spores by AMF, those that have, point towards a positive interaction. With very limited data available on the effect(s) of compost on the extraradical growth of AMF, it is too soon to draw any firm conclusions on this matter. However, this is an important knowledge gap that goes directly to the functioning of the symbiosis, and so deserves further investigation.

Interactive effects of compost and AMF on plant growth and nutrition

One of the most frequently cited reasons for adding compost to the soil is to provide nutrients to enhance plant growth (Hargreaves et al., 2008, Quilty and Cattle, 2011). Equally, the most widely cited benefits of forming AM are enhanced plant nutrition, especially P, and plant growth. A major question that this review seeks to answer is whether or not the application of AMF and compost together provides a benefit to plants in terms of enhanced growth and nutrient acquisition. Further, it also seeks to determine whether or not dual application of compost and AMF provides a greater benefit than that of adding compost or AMF alone.

Question 3. Where compost and AMF were added to the soil together, was plant growth greater than where (a) neither AMF nor compost, (b) only AMF, and (c) only compost, were added to the soil?

In sourcing data to answer this question, it was found that shoot dry weight (SDW) was the most commonly reported measure of plant growth, together with shoot P and N contents. Thus, my emphasis here is on above-ground growth and P and N nutrition.

Based on 42 data pairs from 15 published papers, it was found that the dual application of AMF and compost yielded greater plant growth compared to where neither was added (Figure 2a). When compared to where only AMF were added, dual application resulted in greater plant growth in nearly two thirds of the 55 observations, sourced from 18 publications (Figure 2b). A similar response was seen when dual application was compared to where only compost was applied, based on 54 observations from across 17 published papers (Figure 2c). Taken together these data suggest that dual application of AMF and compost provides superior plant growth compared to where either AMF or compost are added separately. This further supports the assertion that the application of AMF and compost provides a compatible system that yields increased plant growth. [NOTE: INSERT FIGURE 2 HERE. CAPTION: **Figure 2** Change in plant growth (Shoot Dry Weight, SDW) following the addition of compost and AMF together, compared to where **(a)** neither compost nor AMF were added, and **(b)** to where only AMF were added, and **(c)** where only compost was added.]

It is likely that the improvements in plant growth seen with compost and AMF additions were due to enhanced plant acquisition of nutrients (see below). It is interesting to note that dual application of compost and AMF had a generally positive effect on plant growth and colonization of roots by AMF (see above). Although it seems reasonable that if dual application is compatible with the formation of AM then it will also be compatible with the functioning of AM, it is important to note that the extent of colonization is not always well correlated with AM functioning (Smith and Read, 2008), and so this should be treated with due caution. The improvements in growth seen here may also be related to improvements in soil structure associated with compost and AMF addition (see below). To further explore the effect of dual application on plant nutrition the following question was asked:

Question 4: where compost and AMF were added to the soil together, was plant shoot P or N content higher than where (a) neither AMF nor compost, (b) only AMF, and (c) only compost, were added to the soil? The dual application of AMF and compost resulted in an increase in shoot P and N in all studies, when compared to the situation where neither compost nor AMF were added to the soil (Table 2). When compared to the situation where only compost was added, dual application yielded an increase in P and N contents in 89% and 80% of cases, respectively. When compared to the situation where only AMF were added, dual application yielded an increase in P and N contents in 69% and 53% of cases, respectively. Taken together these results indicate that dual application clearly has benefits, compared to the situation where neither compost nor AMF are added. Further, the addition of both together was especially effective when compared to where only compost was added. This suggests that when AMF are added to the soil together with compost, the AMF enhance the capacity of the plants to acquire compost-derived nutrients.

Improvements in plant nutrition with dual AMF and compost application could be attributed to both the release of nutrients from the compost, and/or an improved capacity of plants to acquire nutrients from the soil via their associations with AMF. As noted above, relatively few studies have directly investigated the impact of compost addition on the extraradical growth of AMF, or the ability to colonize compost 'patches' in the soil, or directly acquire mineralized nutrients derived from compost. Irrespective of the mechanisms involved, the improvements in plant nutrition identified here go a long way to explaining the general increases in plant growth observed with the dual application of AMF and compost (see above).

A number of studies have investigated the response of different AMF to the same compost, in terms of changes in plant growth. For example, Alguacil et al. (2004) found that when three different AMF were added to the soil along with compost, there was an increase in the growth of a woody shrub compared to where neither compost nor AMF were added. However, when working with the same fungi and plant species, the same group found that under irrigated conditions there was an increase in growth with the same fungi, and that this was only true for two of the fungi under unirrigated conditions (Caravaca et al., 2005). In another study, in which compost and AMF effects on the growth of four different plant species were investigated, it was found that again responses differed amount plant species (Palenzuela et al., 2002). Together these examples serve to highlight the importance of taking into consideration the differential responses of different AMF and plant species under different conditions. A similar argument can be made for different composts having different effects on plant and AM responses.

An important question that is rarely asked relates to whether or not the addition of nutrients to the soil from compost provides similar benefits to those added from a purely inorganic source. One of the challenges in such studies relates to the establishment of treatments where equivalent amounts of nutrients in different forms (e.g. “plant available” P) are applied either as compost or as inorganic fertilizer. Nevertheless, some studies have done so, with interesting results. For example, El Din et al. (2000) found that with the addition of compost plants had higher levels of mycorrhizal colonization, plant dry weight, N content, P content, and yield, and lower disease incidence, compared to where the plants were supplied with nutrients in inorganic forms. Additional such studies, where appropriate controls are included, may be especially important in demonstrating the field relevance of compost and AM to farmers, and so are encouraged.

Plant growth and nutrition, AMF and compost – conclusions.

The dual application of AMF and compost is clearly compatible, with a clear increase in not only plant growth, but also, plant N and P contents. However, the underlying mechanisms that drive these responses are not well understood. While it seems likely that AMF are able to acquire mineralized nutrients from organic sources (Smith and Smith, 2011), it is not clear if they directly colonize the compost, especially where it is surface applied, or if they rely on mineralized nutrients from the compost to be leached into the surrounding soil. Nevertheless, based on this review of the literature, I conclude that biologically regulated nutrient supply systems based on compost and AM have considerable potential to deliver nutrients to plants.

Interactive effects of compost and AMF on soil properties

Both AMF and composts play an important role in soil aggregation, and thence soil structure. The hyphae of AMF, and indeed other fungi, can bind soil particles together via enmeshment and the release of organic compounds (Rillig and Mummey, 2006). Organic matter, such as compost, can serve as the main binding agent in many soils (Tisdall and Oades, 1982). Thus, it therefore follows that if compost application affects the formation of AM, and the growth of AMF hyphae in the soil (Palenzuela et al., 2002, Valarini et al., 2009), the addition of compost and AMF together may have a greater effect on soil structure, than where they are added to the soil separately. In an attempt to further explore this issue, the following question was asked.

Question 5: where compost and AMF were added to the soil together, was aggregate stability higher than where (a) neither AMF nor compost, (b) only AMF, and (c) only compost, were added to the soil? Before answering these questions, it is important to note that soil aggregation can be measured in a number of ways. After reviewing the literature it was found that the most common used measure of soil aggregation, in the context of compost and AM, was aggregate stability. A small number of studies have also reported changes in Mean Weight Diameter of soil aggregates; both of these measures of soil aggregation are considered here.

When compost and AMF were added to the soil together, there was a strong trend towards increased aggregate stability, compared to where neither was added (Table 3). When dual application was compared to where only AMF were added, there was a near equal number of studies in which aggregate stability either increased or remained the same. However, when compared to the situation where only compost was added to the soil, dual application had no impact on aggregate stability. Very rarely did the dual application of compost and AMF have a negative impact on soil aggregate stability.

Based on available data, it is concluded that while AMF and compost have an impact on aggregate stability, dual application only delivers an additional benefit when compared to application of AMF alone. Given that AMF have a well established role in improving soil structure (Rillig and Mummey, 2006), this may be related to the time scales over which the addition of organic matter, and the enmeshment of soil particles by AMF, operate. When considered in terms of their impact on MWD of soil aggregates, the addition of compost clearly provided a benefit over where neither compost nor AMF were added, or where they were added separately (Table 3). However, relatively few studies have focused on MWD in this context, and so, any conclusions at this stage should be treated with this in mind.

Improvements in aggregate stability may also serve to provide a more favourable growing environment for both plants and AMF. Improved aggregate stability can result in improvements in a range soil physical, chemical and biological properties (Rillig and Mummey, 2006, Six et al., 2004), which in turn has important implications for plant growth and nutrition. These improvements, along with the provisioning of nutrients, may help to explain why compost addition helps to improve plant growth and nutrition, as reported above.

A number of other physical properties of soil have been investigated following the application of compost and AMF. For example, when AMF and compost were added together, bulk density was decreased in seven out of 11 observations (from 7 studies), compared to where neither compost nor AMF were added. However, when compared to where only compost was added to the soil, dual application yielded an increase in seven out of nine observations (from six studies). While only an indication, due to the small sample size, there is a suggestion that the addition of compost together with AMF does not improve soil bulk density compared to the situation where only compost is added. One possible explanation is that compost is often surface applied, whereas AMF are typically mixed in with the soil. While speculative, this highlights the need for further studies, especially those specifically investigating effects of different methods of applying AMF and compost on soil properties.

Soil structure, AMF and compost – conclusions.

While there are relatively few studies that have investigated the dual effects of compost and AMF addition on soil structure, there is some suggestion that dual application may be beneficial. While this benefit was greatest compared to the situation when neither compost nor AMF were applied, there was a signal in the literature that dual application was superior to the application of AMF alone, and to a lesser extent compost alone. Given the time scales over which improvements in soil structure occur, there is clearly a need for longer-term studies of this issue and its consequences for plants and AMF.

Conclusions and Future directions

Certainty in responses of plants, and soils, to compost and AM will need to be underpinned by greater mechanistic knowledge, particularly if biologically regulated nutrient supply systems are to gain wider acceptance. To date, most studies of AM and compost have focused on responses to application, either in terms of the formation of the association, or effects on plant growth, and to a lesser extent plant nutrition. In undertaking this review, a number of key knowledge gaps were identified. It is hoped that listing these knowledge gaps here will stimulate future research in this area.

- Do AMF colonize and acquire mineralized nutrients from within patches of compost, as they do for inorganic nutrient patches (Cavagnaro et al., 2005, Tibbett, 2000, Facelli and Facelli, 2002), or do they acquire mineralized nutrients as they are leached through the soil profile? Answering this question will require further investigation of the growth of AMF hyphae in soils containing compost (Palenzuela et al., 2002, Valarini et al., 2009). It will also be important to determine to what extent AMF acquire compost-derived nutrients. This will be challenging as the labelling of compost with stable and radioisotopes to permit tracing of nutrients along the compost-soil-AM continuum will be complex due to the need to label composting feed-stocks, and the relatively short half-life of some radio-isotopes.

- If AMF acquire nutrients from compost as they are mineralized (Smith and Smith, 2011), then studies that simultaneously investigate shifts in soil microbial communities involved in soil organic matter mineralization following compost addition, and the formation and functioning of AM, will be needed (Powlson et al., 2001).
- Given the tremendous functional diversity that exists in AMF (Cavagnaro et al., 2005, Drew et al., 2003, Smith et al., 2004), it is likely that different AMF will vary in their responses to compost. While some studies have begun to investigate this question (e.g. Caravaca et al., 2005, Pueschel et al., 2011), this is an area ripe for further investigation.
- While short-term studies are valuable, there is a need for longer-term studies that assess the effects of compost and AMF on ultimate agricultural yields, under realistic management conditions. An important point to note here, is that while many farms are using composts, and so this question could be addressed using a survey based approach, it is important that control plots, in which no compost is added, are required as a point of comparison. This will be key if we are to identify the mechanisms that underpin biologically regulated nutrient supply systems based on compost and AM.

The aim of this review was to determine whether or not the use of compost and AMF was compatible. Based on available literature it is clear that the application of compost most often has positive or neutral effects on the formation of the symbiosis, and that dual application of compost and AMF provides clear benefits to plants in terms of growth and nutrition. There is also emerging evidence that dual application also provides benefits in terms of soil structure, but more work in this area is needed. Taken together, the conclusion of this review is that that biologically regulated nutrient supply systems based on compost and AM are compatible. This finding will become increasingly important as inorganic fertilizers become more scarce and expensive. However, for such systems to become more widely accepted, there is a need for greater certainty in plant responses to compost application and AM functioning, and this requires greater mechanistic knowledge.

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Tables

Table 1. Change in abundance of spores of AMF with compost addition

	Increased	Decreased	No change	Number of studies
Change in AMF spores following compost application	16	0	6	5

Table 2. Change in shoot P and N content of plants with the addition of compost and/or AMF.

	Increased	**Decreased**	**No change**	**Number of studies**
Shoot P content				
Compost and AMF added together, compared to where neither were applied.	26	0	0	8
Compost and AMF added together, compared to where only AMF were added.	18	0	8	8
Compost and AMF added together, compared to where only compost was added.	24	0	3	9
Shoot N content				
Compost and AMF added together, compared to where neither were applied.	19	0	0	6
Compost and AMF added together, compared to where only AMF were added.	10	3	6	6
Compost and AMF added together, compared to where only compost was added.	16	0	4	7

Table 3. Change in aggregate stability with the addition of compost and/or AMF.

	Increased	Decreased	No change	Number of studies
Aggregate stability				
Compost and AMF added together, compared to where neither were applied.	11	1	5	8
Compost and AMF added together, compared to where only AMF were added.	8	1	6	7
Compost and AMF added together, compared to where only compost was added.	3	1	13	8
Mean Weight Diameter				
Compost and AMF added together, compared to where neither were applied.	8	2	0	3
Compost and AMF added together, compared to where only AMF were added.	6	0	0	1
Compost and AMF added together, compared to where only compost was added.	5	3	0	2

Figure Legends

Figure 1 Change in mycorrhizal colonization of roots (per cent root length colonized) following the addition of **(a)** compost, compared to where neither compost nor AMF were added, and **(b)** compost and AMF were added, compared to where only AMF were added.

Figure 2 Change in plant growth (Shoot Dry Weight, SDW) following the addition of compost and AMF together, compared to where **(a)** neither compost nor AMF were added, and **(b)** to where only AMF were added, and **(c)** where only compost was added.

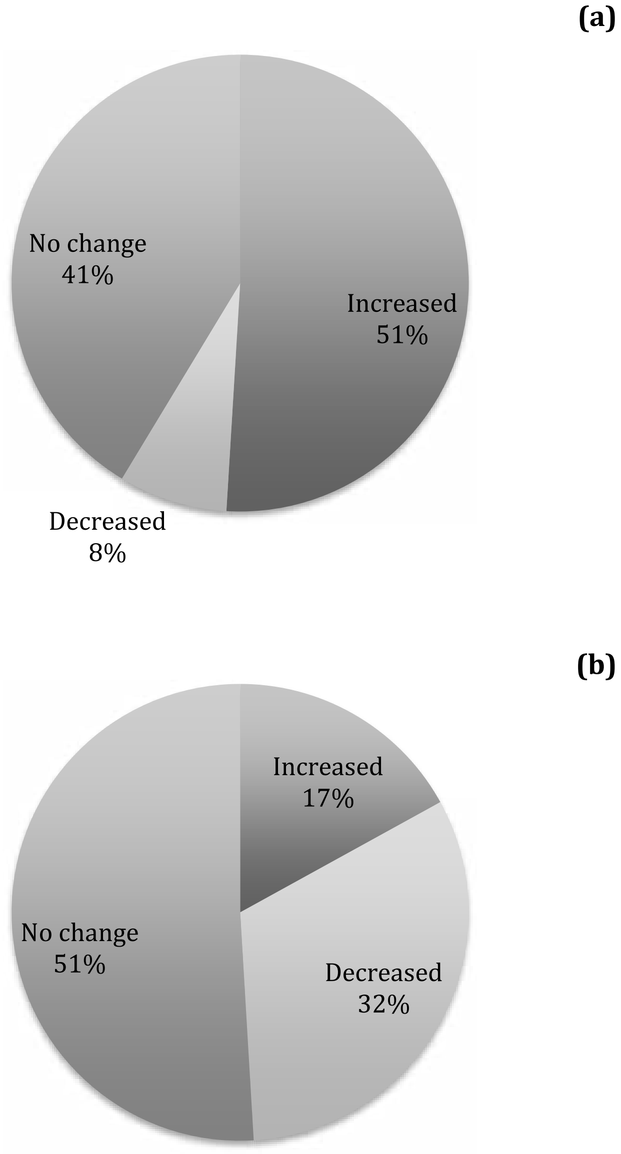
(a)
No change 41%
Increased 51%
Decreased 8%
(b)
Increased 17%
No change 51%
Decreased 32%

Figure 1.

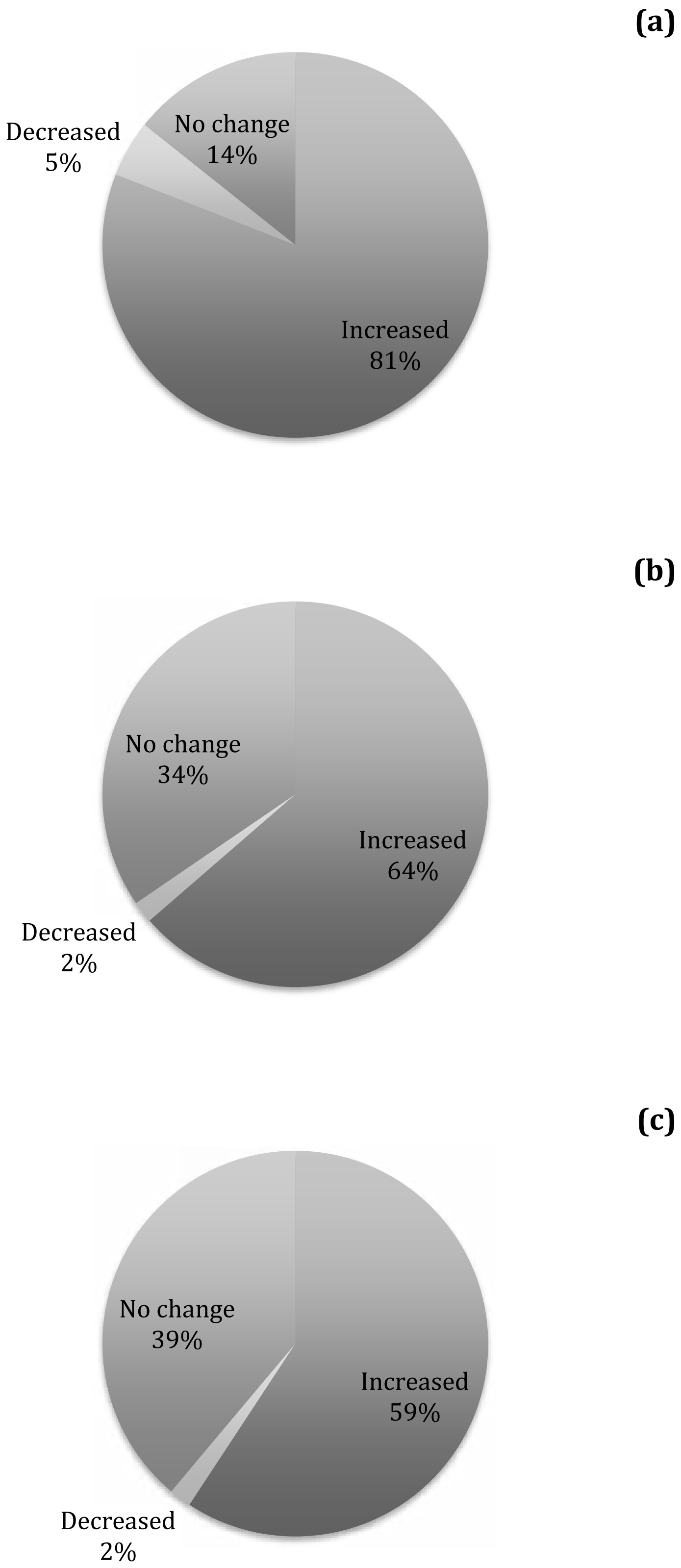
(a)
Decreased
5%
No change
14%
Increased
81%
(b)
No change
34%
Increased
64%
Decreased
2%
(c)
No change
39%
Increased
59%
Decreased
2%

Figure 2.