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Improving Activity of Native Arbuscular Mycorrhizal Fungi (AMF) for Mycorrhizal Benefits in Agriculture: Status and Prospect

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Abstract

Agricultural importance and ecological implications of arbuscular mycorrhizal (AM) symbiosis with land plants are well known. AM symbiosis facilitates plant growth through enhancing uptake of several macro- and micro-nutrients of low mobility in soil, like phosphorus, zinc, copper etc. Beside nutritional benefits to plant, AM also contributes to numerous ecological advantages like influencing microbial and chemical environment of the mycorrhizosphere, stabilizing soil aggregates, conferring tolerance (plant) to several abiotic and biotic stresses, bioremediation of soil and supplying protective (antioxidants) nutrient components to human being through agricultural products (food). There are two approaches to exploit arbuscular mycorrhiza for crops: (1) soil introduction of non-native inoculum and (2) exploitation of native AM fungal (AMF) population. The approach of soil introduction of non-native inoculum of selected AMF to field crops suffers from (i) cost intensiveness, (ii) inconsistent competitive performance of introduced inoculum due to lack of adaptability to new ecology and (iii) negative ecological consequences in terms of possible introduction of invasive species as unintended contaminants. Exploitation of native AM fungal (AMF) population of soils, keeping it undisturbed by avoiding faulty agricultural practices, is an alternative approach, now promoted for sound ecological management of crop production, particularly under stressful situations. The approach is based on twin attributes of AM symbiosis – ubiquitous nature and lack of host specificity of AMF. Several prospective avenues of enhancing native AM activities through agronomic manipulations of crop management practices and cropping systems for enhanced response to diverse native AMF population have been discussed in the present article

Keywords: Arbuscular mycorrhiza; AM inoculums; Crop rotation; Phosphorus; Tillage

Introduction

Inefficient acquisition of less mobile nutrients (like phosphorus, zinc, copper etc.) by crops is one major constraint of agriculture, particularly under rainfed ecology, prone to drought, occurring in various crop growth stages [1]. This reduces nutrient uptake, particularly the major nutrient of phosphorus (P) by plants [2,3]. The available 'non-occluded soil P' (inorganic P) remains in continuous equilibrium between 'solution P pool' which is readily available to plant and 'labile P pool' that remains adsorbed on soil surface and needs root interception for its acquisition by plant [4]. This 'labile P pool' is accessed by mycorrhizal plants through interception by extraradical (external) mycelial network extended beyond root zone that may extend up to several centimeters out in the soil [5] and help plant to acquire P beyond P depletion zone around root [6] which is otherwise not available to plant. Evidence of releasing nutrients from insoluble forms of inorganic sources like mineral particles and rock surfaces by AMF is conflicting [7]. Although there are some reports supporting mobilization of insoluble nutrients by AMF these effects could depend upon synergistic interactions with other P-solubilizing micro-organisms growing endosymbiotically with AM plants [8]. Other beneficial soil microbes like N fixing bacteria and P solubilising bacteria, may synergistically interact with AM fungi and thereby benefit plant growth [9].

Beside nutritional benefits to plant, AM also provides numerous ecological advantages like influencing microbial and chemical environment of the mycorrhizospher, more precisely the hyphosphere, the zone surrounding individual hyphae [10], stabilizing soil aggregates, conferring tolerance (plant) to several abiotic and biotic stresses, bioremediation of soil and supplying protective (antioxidants) nutrient components to human being through agricultural products (food) contributing a key role in the earth's ecosystem services [11].

AM fungal association may influence bacterial communities associated with the roots in both direct and indirect ways [10]. While the fungus provides directly energy-rich carbon compounds derived from host assimilates, which are transported to the mycorrhizosphere via fungal extraradical hyphal network, changes in pH of the mycorrhizosphere induced by the fungus, competition for nutrients, and fungal exudation of other inhibitory or stimulatory compounds induces indirect interactions in the form of mycorrhiza mediated effects on host plant growth, root exudation and soil structure.

The extraradical mycelial network of AMF also imparts binding action on the soil and improves soil structure. In addition, the secretion by AM fungi of hydrophobic, 'sticky' proteinaceous substances, known as 'glomalin' [12], also contributes to soil stability and water retention [13]. The combination of extraradical mycalial network and glomalin secretion is considered to be an important element for stabilization of soil aggregates [14], thereby leading to reduced soil erosion and increased soil structural stability and quality [13].

AM association has been proved to be beneficial to agriculture under abiotic and biotic stressed environment including drought

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(abiotic) and pathogen infection (biotic). AM, under moisture stress benefits in two ways by increasing (i) moisture retention property of soil [15] and (ii) greater exploration of soil moisture [16]. Subsequently, Ruiz-Lazano et al. [17] suggested involvement of modulating drought-induced genes of AM plant in imparting drought tolerance.

Despite several reports of pathogen (soil borne) suppression by AM fungi [18], the underlying mechanism is still not well understood. Some possible mechanisms could be (i) improvement of plant nutrition and competition for photosynthates [19], (ii) AM induced stimulation of saprotophs and plant growth promoting microbes [20], (iii) AM induced anatomical and morphological changes in root system and (iv) AM induced local (at infection site) elicitation of plant defence mechanism [21]. However, additive pathogen suppressing effect of combined application of other antagonistic microbes with AM indicates possible function of AMF as vectors for the antagonists [10].

Improvement of nutritional quality in plant products as a result of mycorrhizal association was demonstrated in lettuce [22]. Such AM induced improvement was found to be dependent on phosphorus sources also. While copper, iron, starch and protein concentrations were increased in lettuce leaves under application of water insoluble P source, water soluble source increased mostly nonstructural sugars. The role of AMF in soil bioremediation, however, is mostly through encouraging associated microflora directly involved in bioremediation [23] as compared to direct role of ecto-mycorrhizas.

The well-drained, aerobic soil conditions of upland ecology supporting native AM activities [24] indicated that AM has greater potential in this ecology. Benefits from AM fungi (AMF) can be accrued by exploiting native AM flora or by application of external exotic inoculum. The former approach is considered to be more effective [25] owing to its stronger ecological adaptation and suitability due to less negative ecological consequences [26]. Thus, AMF inoculum developed from native sources is considered to be more efficient [27] and also cost effective. So, attempts have been made in the present article to discuss possible options of exploiting native AMF by enhancing its activity through (i) manipulations in agro-practices, (ii) adoption of AM supportive cropping systems/rotations and (iii) development and application of AMF inoculum of native origin.

Options for Exploiting Native AM Fungi

Manipulation in agro-practices

Optimizing tillage schedule: Tillage is one important agricultural operation that influences activities of native AMF in soil. Off-season tillage is an agronomic recommendation for management of weed and soil borne plant pathogens. On the other hand, this operation results in soil disturbance induced (SDI) deleterious effects on natural AMF by disrupting established mycelial network [28] leading to delayed colonization in subsequent crops and less P acquisition. Disruption AMF mycelia network in soil causes a delay in the colonizing roots of the next crop, because more time is needed for the inoculum around the roots to accumulate. Tillage induced reductions in mycorrhizal activity and phosphate nutrition is well known in corn [29], and the effect could be replicated in laboratory systems [30] for confirmation. The timing of the reduction in colonization is important, because the crop demands adequate phosphate early in the season for yield potential to be reached [31]. Hence, a compromise between no-tillage (most suitable for native AMF) and optimum tillage for accruing both mycorrhizal and agronomic benefits was felt to be worked out for recommendation. Magnitude of SDI effects depends upon length of undisturbed period (no-till period) [32,33] and degree of soil disturbance in terms of extent of soil pulverization [34]. Under temperate ecology of Canada, 'reduced tillage' (only spring disking) was observed to have less severe negative impact on the abundance of soil hyphae and mycorrhizal colonization in corn by native AMF than 'conventional tillage' (fall mould-board ploughing + spring disking) [35]. A threshold of undisturbed period in terms of maintaining gap between two consecutive tillage operations (using bullock drawn country plough, tilling up to a depth of 10-15cm) of 13 weeks has been worked out for rainfed uplands of eastern India (tropical ecology) [36]. Having maintained this gap, two options of off-season tillage schedules (summer tillage alone and initial tillage after harvest + summer tillage) have been recommended for rainfed, mono-cropped (rice), upland ecosystem under study for maintaining optimum activities of native arbuscular mycorrhizal fungi. Heavy tillage both in terms of frequency and use of fine pulverizing machine reduced size of post tillage soil blocks. Resultant (post tillage) soil cutting blocks less than 4 cubic cm reduced AM induced P uptake in maize [34]. Thus, maintaining both (i) threshold of undisturbed period and (ii) use of coarser pulverizing machines are important for sustenance of native AMF activities in soil.

Optimizing P amendment: Higher soil P concentration was observed to reduce AMF activity [37] probably by reducing root colonization due to reduced root membrane permeability resulting in decreased loss of metabolites [38]. At the same time, plant rich in P are poor in carbohydrate content which reduces AMF colonization [39]. Effects of plant tissue P concentration on AMF colonization, however, is dependent on nitrogen (N) concentration. Root colonization remained unaffected with increasing P concentration when plants were N deficient, but increasing P inhibited mycorrhizal formation when plants were N sufficient [40,41]. Corroborating these findings, P fertilization was also observed to reduce mycorrhizal development in several crops [42,43]. P amendment through organic sources, however, did not adversely affect AMF activities possibly by improving soil biological properties favoring AMF [35]. Since organic manure is not available in required quantity everywhere, optimum dose of inorganic P, supporting maximum native AMF activities, without sacrificing crop yield, for each crop-ecosystem (at micro-level) combination is needed to be worked out. In a similar attempt, P optimum of 20 kg P2O5/ha was worked out for upland rice under AM supportive, two years crop rotation of maize (*Zea mays* L.) relay cropped by horse gram (Dolichos biflorus L.) in the first year followed by upland rice in the second year' [44] as compared to the recommended dose of 30 kg P_2O_5/ha. This P optima, however, was not effective under rice mono-cropping because soil P concentration threshold for maximum benefits from the AM symbiosis were observed to be lower than P concentration threshold for maximum plant benefit without enhanced AMF activities (inoculation) in crops like *Phasiolus mumgo and Triticum aestivum* [45].

Adoption of AM supportive cropping systems/rotations

Reduction in AMF population under fallow (no crop) due to 'fallow disorder' was confirmed by several workers [46,47,48]. Even, contrary to the earlier speculations [49] and subsequent report [50], growing non-host (to AMF) crops, as compared to fallow, not only maintained better AMF activities in terms of colonizing the succeeding host crops [51] and spore population of native AMF [52], in certain cases, pre-cropping of non-host crop like oilseed rape (*Brassica napus* L) significantly increased colonization in succeeding host crop like barley (*Hordeum vulgare* L.). This can be attributed to the previous findings that AM fungal hyphae can make some hyphal growth around the roots of non-host plants without colonizing the roots due to absence of signals from non-host roots required by AM fungi for successful colonization [53]. Such roots surrounded by AM hyphal growth are more efficient in colonizing host plants than chlamydospores or other inoculum source [51]. Such phenomenon is also influenced by soil P level. In non-host Swedes, although not infected by native AMF, magnitude of spore associations was found to be similar as that of host crops like barley and potato [49] grown under both low and high doses of P. The intermediate P level, however, increased spore population only with host crops (barley and potato) indicating the intermediate dose to be P optimum for maximum native AMF activity under AM favorable/ supporting environment (barley and potato rhizosphere).

Mono-cropping of a particular crop leads to narrowing of AMF species diversity index [54] and distribution of AM fungi [52] due to obvious reason of encouraging a particular species favored by the particular crop in continuity without any break [55]. Apart from adverse ecological consequences of reducing AMF diversity, mono-cropping also was reported to reduce proliferation of AMF population than mixed cropping [56,57] due to three main reasons: (1) higher root density under mixed cropping favors AMF multiplication [58], (2) higher plant density exhausting soil nutrients faster stimulates AMF activities in soil [59] and (3) under mixed cropping with legumes, the companion crops get additional nitrogen from the legumes through AM fungi and thereby favoring AMF colonization [56].

Having information on 'fallow disorder' and adverse effects of mono-cropping on AMF, improving native AMF efficiency for enhancing P nutrition of crops through removing or reducing the factors (fallowing and mono-cropping) favoring these disorders/ adverse effects were thought of. The factors could be removed/reduced by increasing cropping intensity through introduction of AM supportive crops, suitable to specific ecology, in the cropping rotation or cropping system. Several crop combinations suitable to various ecologies were evaluated by different researchers under diverse ecologies worldwide for the purpose. Native AMF population build up varied with different cropping regimes in the same soil under temperate [49,60] and tropical climates [58,61].

While enhancement of mycorrhizal colonization resulting in improved nutrient (P) uptake by cereals under mixed cropping of 'cereals - non-legumes' or 'cereal - cereal' combinations like rice (*Oryza sativa* L.) – finger millet (*Eleusine coracana* L. Gaertn) [62] was attributed to higher root density per volume of soil favoring the spread of the symbiotic fungi [60], higher root volume coupled with N backup to the symbiotic system in 'legume – legume' combination, like of berseem clover (*Trifolium alexandrinum* L.) – Persian clover (T. *resupinatum* L.) [63], and 'cereals – legumes' combination like maize (*Zea maize* L.) – berseem (*T. alexandrinum* L.) [64], rice (*Oryza sativa* L.) – pigeon pea (*Cajanus cajan* L.) [62] and rice – peanut (*Arachis hypogea* L.) [57] led to additive mycorrhizal benefits in terms of nutrient uptake and growth promotion. Ability of AM fungi to interconnect crop species grown together might allow translocation of N from legumes to cereals in mixed cropping.

Continuous mixed cropping of 'cereal – legume' and 'legume – legume' combinations, however, enhances chances of developing sick-plot of soil-borne plant pathogens, mostly for legumes, particularly under rainfed agro-ecosystem having mono-modal rainfall pattern with single annual crop season. For this ecology, crop rotations are safer options. Advantages of crop rotations in terms of mycorrhizal benefits can be attributed to (1) soil mycorrhizal potential left by both non-host and host pre-crops [65,66,67,61] and (2) reducing 'fallow disorder' [61]. The residual soil mycorrhizal potential of the pre-crop is also long-lasting as evident from the resulting mycorrhizal benefits drawn by mycorrhiza responsive crop like sugarcane even after 2-4 years cycle [68]. Such residual effects can also be exploited under comparatively less AMF-favorable ecology like wetland rice with anaerobic soil condition. Pre-cropping rice seed bed (dry seedbed) with several host crops like fodder varieties of maize, sorghum (*S. bicolor*), Dinanath grass (*Pennisetum pedicilliatum*), finger millet (*Elusin indica*) and little millet (*Panicum miliare*) enhanced AMF colonization of rice seedlings and P uptake [69] after transplanting at maturity under rainfed conditions. In pre-colonized roots, AMF remained dormant during inundated period and became active during intermittent drought periods [70] leading to moisture stress which is very common under rainfed ecology.

Development and application of AMF inoculum of native origin

Practical and ecological advantages of native AMF inoculum over that of non-native one have been discussed in the previous chapter (Introduction). AMF inoculum developed from native source are more effective [71] mainly due to its ecological adaptation beside other advantages of less negative ecological consequences in terms of possible invasive species introduction as unintended contaminants [26] and cost effectiveness. Having known these advantages, developing AMF inoculum of native origin has been thought of. Several small scale inoculum production techniques developed by different researchers, time to time, have been reviewed by Marleen et al. (2011) [72]. In the present review we have emphasized on various on-farm protocols for mass-production of native AMF inoculum suitable to various agro-eco systems. Soil-root based AMF inoculum produced by (i) growing pre-colonized (by native AMF) Bahia grass (*Paspalum notatum* Flugge) on fumigated plots [73] or raised beds amended with vermiculite and compost [74], (ii) multiplying native AMF fungal consortium on Sorghum roots (*Sorghum bicolor*) grown in partially sterilized (by soil solarization) [75] have been effectively used respectively as amendment to horticultural potting media for production of vegetable seedlings and as band placement in field for growing direct sown upland rice. A more recent approach of multifunctional microbial consortium inoculum facilitates integrated crop production system. The microbial consortium may include combination of compatible beneficial microorganisms having various plant growth promoting and pest controlling functions catering to the diversified crop cultivation need by one inoculum. Co-inoculation of multifunctional microorganisms combinations like (i) AMF + PGPR + PSB in lettuce [76], (ii) AMF + PGPR (*Azospirillum, Azotobacter, Pseudomonas* etc.) in Rhodes grass (*Chloris gayana* Kunth) [77], (iii) AMF + PSB in clover [78] and in English mint (*Mentha piperita* L.) [79] not only expressed individual beneficial effects, also resulted in additive or synergistic effects on plant growth promotion. Such results prompted the researchers to develop microbial consortium inoculum. In this effort many microbial consortium inoculum have been developed, tested [80] and commercialized. Integration of native AM supportive components is likely to produce additive or synergistic effects on plant growth promotion. In such effort, integration of AM supportive components of (i) crop rotation and (ii) application of on-farm produced native AMF inoculum under blanket practice of optimum tillage schedule and P amendment enhanced native AMF activity, P uptake and grain yield of upland rice under rainfed ecology [62]. Further validation, however, are required for their efficiency under farmers field condition for assessing technical feasibility and necessary fine tuning. While producing AMF inoculums of native origin, however, precautions should be taken to check the efficacy of the mixed fungal composition in terms nutrient acquisition and growth improvement of the target crops.

Conclusion

Possibilities of exploiting native AMF for mycorrhizal benefits in agriculture through several eco-friendly avenues including manipulation of agro-practices, crop rotations and application of native AMF inoculum was well documented and their practical feasibility has been validated for adoption and recommendation as integrated crop production component. The following suggestions have been made to further strengthen the research for harnessing additional benefits from native AMF and other beneficial microorganisms for developing more ecologically sound integrated crop management strategy.

1. Location, soil type and agro-ecosystem specific optimum tillage schedule and type in terms of tillage depth and pulverization (favoring native AMF/supporting minimum damage to native AMF) need to be worked out at micro level for location specific recommendation.
2. Development of soil fertility and agro-system based prediction model of mycorrhizal activity would provide basis for regular updating of location specific fertilizer and microbial inoculums amendment schedule as recommendation which would reduce cost of cultivation beside mycorrhizal advantages.
3. Farmers' wisdom need to be considered for fine tuning suitable AM supportive crop rotation recommendations with the help of extensive farmers' participatory on-farm trials.
4. Further refinement of native AMF based inoculum production protocol in terms of quality, longevity and broader ecological adaptability would make the technology more suitable.
5. Inclusion of multifunctional microorganisms like bio-controlling (pests) agents beside biofertilizer agents in the microbial consortium inoculum would strengthen ecologically sound crop management strategy.
6. The research on native AMF aided agricultural benefits needs to be integrated with exploiting other beneficial microorganisms.
7. Strengthening research on integration of beneficial microorganisms' supportive agricultural components followed by proper validation under farmers' participatory mode would result in tangible recommendation as component of integrated crop management strategy.

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