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Allelopathic principles for sustainable agriculture

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CONTENTS

"*The success or failure of our civilization will be determined by the success of Agricultural Science to meet our needs of food, fiber and feed.*" Anonymous

ABSTRACT

Allelopathic research in past few decades has shown the feasibility of weeds and plant diseases management by allelopathic crop plants, plant residues, cultural manipulation, microorganisms as bioherbicides, and rhizobacteria. Inconsistency between the effectiveness of plant growth-promoting rhizobacteria (PGPR) to stimulate the plant growth and yield in the laboratory and the field has been reported. This inconsistency in the field results from PGPR applications can only be remedied through the improved knowledge of interplay between the host and introduced PGPR inoculant in the rhizosphere under field conditions. Application of biofertilizer reduced the quantity of chemical fertilizer used for maintaining threshold levels of crop productivity. We hope this review will stimulate further research in a holistic approach to solve the agricultural problems and achieve economically profitable and environmentally benign sustainable agriculture.

Key words: Allelopathic crop plants, biocontrol of plant diseases, biofertilizer, bioherbicide, diazotrophs, plant growth-promoting rhizobacteria, plant residue, rhizobacteria, weed management.

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1. INTRODUCTION

Allelopathy is a complex interaction among plants, as well as among plants and microorganisms, through biochemicals released into the environment either actively (e.g. exudates) or passively (e.g. leachates or decay). Although the phenomenon was noted almost since the inception of civilization, for example "soil sickness" following some crops, scientific evidence was lacking until Molisch published his book "Der Einfluss einer Pflanze auf die andere Allelopathie" in 1937 in which he coined the word "allelopathy." Allelopathy was generally ignored until 1974 when Rice published the book "Allelopathy" based on his research on the succession of vegetation and revived the science (175). In his last book "Biological Control of Weeds and Plant Diseases Advances in Applied Allelopathy," Rice emphasized the biocontrol of agricultural pests (178). Rice advocated a holistic approach in the application of allelopathic principles for reduction of agrochemical input in farming systems. Allelopathy research over the past several decades provides useful information to address some agricultural problems.

The goal of allelopathy research is to maximize the utilization of locally available natural resources in agriculture and forestry, thereby reducing agrochemical inputs, while maintaining economic productivity without degrading the environment, leading to sustainable agricultural systems. Strategies of allelopathy research for promoting the low agrochemical input agriculture include: (A) Pests management (weeds, plant pathogens and other pests) by biological means, and (B) utilization of available natural resources (e.g. biofertilizers) to enhance the soil fertility status. In spite of the use of pesticides and other management practices, weeds and plant diseases still significantly reduce crop yields and thus pest management has a high priority in sustainable agriculture. Adequate nitrogen availability is crucial in crop productivity; an input of 1 kg/ha N-fertilizer can increase cereal production by 10 kg/ha. Biological N-fixation (BNF) accounts for 65% of nitrogen currently used in conventional farming system and rhizobial-legume systems contribute a major portion of BNF. Associative diazotrophs contributes the BNF for particular crops with appropriate soil nutrient status. Azolla (aquatic fern)-cyanobacteria symbiosis contributes substantial amounts of nitrogen to rice plants cultivated in flooded areas. [Biological N-fixation is not discussed here. The reader is referred to Mallik (130) for legume-rhizobium symbiosis and Mallik and Williams (133) for associative N-fixation.] Biofertilizer has received great deal of attention during the last 2 to 3 decades owing to public environmental awareness, human and live stock's health issues, fertilizer costs (particularly for farmers in developing countries), and growing interest in organic farming and greater demand for organic products. Application of biofertilizers can substantially reduce or eliminate synthetic fertilizer use, improve soil properties, and promote soil microbial balance.

No ecosystem can exist without microorganisms. Plant and microbial interactions occurs in the vicinity of roots (rhizosphere). Soil bacteria that aggressively colonize the rhizospheres by displacing native root colonizer are called rhizobacteria (191). These bacteria sustain high population densities throughout the host-plant's ontogeny (14). Although sustained progress in rhizobacterial research has been made during the last two decades, the use of rhizobacteria as plant growth promoters, as well as biocontrol agents for plant pathogens and weed control, has not been fully exploited.

This review summarizes the advances made using the allelopathic plants and microbes to promote sustainable agriculture. References cited here are exemplary and an exhaustive review of literature is not intended. Rather we hope to stimulate further research in this area for exploitation of the available plant and microbial resources for use in low agrochemical input farming systems.

2. BIOCONTROL OF PLANT PESTS

Environmental concerns and high pesticide costs have stimulated the research on biological (non-pesticide) means for pest control. Agricultural systems must be compatible with local ecological, economical and cultural conditions to preserve biotic diversity, habitat stability and production sustainability. A very important component of sustainable agriculture is the management of plant diseases and weeds, either by reducing pest-populations or by inducing self-defense systems within the crops. Plant diseases reduces the crops yields by about 20% (152) and weeds by 10-25% depending on the region of world (1,6). Development of herbicide-resistant weed species adds another dimension in the difficulty of weed management. World-wide, 156 weed species (94 dicots and 62 monocots) developed the herbicide resistance (79). Rye grass [*Lolium rigidum* (Gaud)] has evolved resistance to six herbicide classes (164). Pesticides currently used are broad spectrum chemicals that affects both targets and non-target species. Although pesticide application is crucial for greater crop production, adverse impact of chemically intensive agriculture on the environment is a concern. The integration of bio-management of pests with local, traditional systems can substantially reduce the quantity of pesticides used and help to develop eco-friendly, sustainable farming systems.

2.1. Weeds

Efficient weed management plays a key role in agro-ecosystems. Allelopathic weed management strategies are: the use of allelopathic crops, cultural practices as smother crops and their disease causing microbes. Allelopathic research during the last half a century has shown the possibility of developing weed resistant crop plants (allelopathic crops). Cultivars of several crops allelopathic to weeds have been reported. Genetic variability in weed suppressive traits of several crops, including barley (*Hordeum vulgare* L.), sunflower (*Helianthus annuus* L.), sorghum [*Sorghum bicolor* (L.) Moench.], rye (*Secale cereale* L.), corn (*Zea mays* L.), rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.), has been reported (17).

2.1.1. Allelopathic rice: Allelopathic rice germplasm has been reported from Australia, China, Egypt, Korea, Japan and India. Dilday *et al.* (43) reported that several rice germplasms were allelopathic in field tests to duck salad [*Heteranthera limosa* (SW) Wild.], redstem ammania (*Ammannia coccinea* Rottb.) and barnyardgrass [(*Echinochloa crusgalli* (L.) Beauv.]. The allelopathic rice accessions produced 2 to 3 times more root biomass than the non-allelopathic accessions. The yield reduction in barnyardgrass infested soil was 37% for allelopathic rice accessions compared to 60 to 68% reduction in yield of the non-allelopathic rice accessions. After comparing physiological performance of allelopathic and non-allelopathic rice cultivars, it was concluded that there was no extra

[*] Common and scientific names for weeds have been standardized using the Weed Science Society of America's Composite List of Weeds found at http://www.wssa.net/Weeds/ID/WeedNames/namesearch.php. Accessed October 28, 2008.

physiological cost to the allelopathic rice cultivars for weed-suppression (157,158,221). Allelopathic rice cultivars are competitive against weeds for light and nutrients, and have other characteristics including greater plant height, more rapid growth, active rooting and larger biomass. These are in general the characteristics of allelopathic crop plants (202). Song *et al.* (199) reported that root exudates of allelopathic rice cultivars at different phenological stages contained benzene and phenol derivatives, benzoic acid, phthalic acid and several long chain fatty acids. The root exudates containing these allelochemicals significantly reduced the barnyardgrass height, tiller number and dry weight when compared with non-allelopathic varieties. Allelopathic rice cultivars exuded 3-hydroxy benzoic acid (HBA), 3,4–dihydroxydiscinnamic acid (3,4-DHHCA), and 4-hydroxyphenylacetic acid when grown in flooded or upland conditions, while 4-hydroxy benzaldehyde (4-HB), 3 hydroxy,4-methoxybenzoic acid (3-H, 4-MBA), and 4-hydroxycinnamic acid (4-HOA) were exuded only when the rice was grown in upland conditions (136). It is suggested that these allelochemicals contributed to duck salad growth inhibition. Allelopathic inhibition of barnyardgrass and duck salad growth by rice is genetically controlled and varies among cultivars (92).

2.1.2. Wheat and Barely: Differential allelopathic activity of wheat varieties against rye grass has been reported suggesting that wheat allelopathy is genetically controlled (231,232). After identification of the gene, or genes (multiple gene involvement is most likely), it might be possible to incorporate the allelopathic trait by gene transfer to another desirable wheat cultivar. Hashem and Adkins (78) found a wild wheat (*Triticum speltoides* L.) accession that suppressed the wild oat (*Avena fatua* L.). Copaja *et al.* (40) reported wide variation in production of DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) in Chilean wheat cultivars (*T. aestivum* L. and *T. durum* Desf.). Similar variation in gramine content in barley was reported (127). The alkaloids (gramine and hordenine) from a barley cultivar inhibit white mustard (*Sinapis alba* L.) growth. Additionally, hordenine affects growth of army worm (*Mythimna convecta*), a noxious pest of barley, and a fungal pathogen (*Drechslera teres*) (126). Fay and Duke (54) reported differential allelochemicals production in common oat (*Avena sativa* L.) accessions; four of 3000 accessions screened produced 3-times as much scopoletin (6-methoxy-7-hydroxy coumarin) as a standard cultivar.

2.1.3. Cucumber: Putman and Duke (166) reported allelochemicals variations among the cucumber (*Cucumis sativus* L.) cultivars in 1974. Coupling the natural variation of these compounds and their genetic manipulation into crop plants provides a means of weed suppression that will reduce our dependence on chemical weed control. The use of allelopathic crop plants as cover or smother crops provides a further means of non-chemical pest control.

2.1.4. Cover or Smother Crops: Cover or smother crops are grown in the field and mowed or incorporated into the soil prior to sowing of the main crop. Besides suppressing weed growth, cover crops increase organic matter content, add soil nutrients, improve soil physical properties, and reduce soil erosion. Hairy vetch (*Vicia villosa* Roth) is a popular cover crop, due to its rapid growth and allelopathic potential, and is used both in grain and vegetable production. Hairy vetch as a cover crop reduced weed density by 70% and biomass production by 50 to 70%, compared with fallow land (203). Fujii (61) reported that weed suppression by hairy vetch is comparable with rye and oat (Table 1). Some most efficacient cover crops are buckwheat (*Fagopyrum esculentum* Moench), foxtail millet (*Setaria italica* (L.), rye, sorghum, alfalfa (*Medicago* L.), sunflower and cruciferous plants, (56,118,119,148,156,165, 190,215,229).

Table 1. Effects of fall-sown cover crops on weed suppression.[1]

Cover crop	Weed Contro (%)	Biomass (g/m^2)
Cereal rye	99	1182
Wheat	99	1751
Oat	99	1210
Barley	99	1173
Hairy Vetch	99	994
Birdsrape mustard	97	834
White mustard	95	416
Alfalfa	77	384
Rice straw mulch	87	1000
Herbicide Treatment (benthiocarb + prometrin 40 kg/ha)	91	-

[1]Data are pooled from several experiments done in Japan in 2001 (61).

Evaluation of weed suppressive ability of different summer and winter crops in India showed that the order of weed suppression for summer crops was: pearl millet [*Pennisetum glaucum* (L.) R. Br.] > maize > sorghum > cowpea [*Vigna unquiculata* (L.) Walp], while the order of suppression for winter crops was: berseem (*Trifolium alexandrinum* L.) > oat> lentil (*Lens culinaris* Medic.)> wheat (149). Although all 13 pearl millet genotypes reduced the weed population, which included Chinese tallowtree (*Trianthema portulacastrum* L.) and pigweed species (*Amaranthus* sp.), nine of the genotypes significantly reduced total weed population and one genotype (HHB 67) suppressed 75% of the Chinese tallowtree population when compared to the control. Similar variability in the suppression of weed growth by Indian mustard [*Brassica juncea* (L.) Czen.] and rapeseed (*Brassica napus* L.) genotypes was reported by the same author. All the accessions of Indian mustard suppressed common lambsquarters (*Chenopodium album* L.) and littleseed canarygrass (*Phalaris minor* Retz.) growth by 80 %. These examples suggest that selection of crop genotypes for weed suppression may be worthwhile.

2.1.5. Crop Rotation: The practice of traditional crop rotation declined with the onset of industrial agriculture. However, it is being reconsidered for the development of environmentally sound and sustainable farming systems. Rotating crops with different planting dates and growing periods reduce the population density of weeds. Additional benefits of well designed crop rotation include reduction of pathogens, insect populations, and weed seed banks. Crop rotation is an important tool in reducing weed seeds in the soil and seedling development (122). The population density of the downy brome (*Bromus tectorum* L.) remained low and stable when winter wheat was rotated with rapeseed, but the weed population increased when winter wheat was grown continuously (24).

Schreiber (190) reported that soybean-wheat-corn rotation in no-till or reduced tillage significantly reduced giant foxtail (*Setaria faberi* Herrm.) population in a comparison to continuous corn crop.

2.1.6. Companion Cropping: Companion cropping was more effective in reducing weed populations than a crop monoculture. Companion crops utilize the available resources more efficiently and reduces the competition from the weeds. Putnam and Tang (167) reported a few examples from the Russian literature on growth promotion due to companion seeding. Co-seeding legumes in a corn crop promoted corn yield. White mustard and wild European heliotrope (*Heliotropium europapeum* L.) co-planting enhanced the yield of several crops and reduced weed population and insect pests. Intercropping cereals with forage legumes such as red clover (*Trifolium pretense* L.) or alfalfa was a common practice in the U.S. for suppression of cool season weed couch grass [*Elytrigia repens* (L.) (50).

2.1.7. Crop Residues: Application of crop residues for weed suppression has been recently reviewed (113,114,148). The allelopathy literature provides extensive information on the potential of sorghum, rye, vetch, crucifers, and sunflower residues to suppress weed growth. Alfalfa pellets (made from alfalfa shoots, 15g/pellet) used as feed for livestock when applied to rice fields at 100kg/1000 m^2 significantly reduced weed biomass when compared to the control and suppressed the common paddy weeds like watergrass [*Echinochloa oryzicola* (Vesinger) Vesinger], monochoria [*Monochoria vaginalis* (Burm. f.) Kunth] and smallflower umbrella sedge (*Cyperus difformis* L.) (235). The pellet application was as effective as an herbicide treatment and had no negative impact on rice growth. Incorporation of the pellets at 1-2 t/ha within 5 days after rice transplantation was recommended for maximum weed suppression. However, application of the pellets at 1 t/ha may not be feasible in practical terms (235). Application of alfalfa residues was reported to reduce redroot pigweed (*Amaranthus retroflexus* L.), common lambsquarters, crabgrass (*Digitaria sanguinalis* Haller), and velvetleaf (*Abutilon theophrasti* Medik.) growth (37). Dyke and Liebman (49) found that incorporation of crimson clover (*Trifolium incarnatum* L.) incorporated into the soil reduced biomass production of common lambsquarters but had little effects on the growth of sweet corn. Soil incorporation of white mustard residues before planting potato (*Solanum tuberosum* L.) significantly reduced weed density and weed biomass (29). A similar effect was reported in a pea (*Pisum sativum* L.) production system (2). A few weeks between residues application and planting is desirable to allow the toxicity of residues to decline before crop seed germination and seedling establishment, which reduces the chance of toxic affects on the crop plant (41). Velvet bean [*Mucuna pruriens* var. *utilis* (L.) DC] has a considerable potential as weed suppressor and contains the allelochemical L-3,4-dihydroxy-phenyl amine (L-DOPA) (60). Buckwheat has been reported to be an effective weed suppressor. Applied at 1-2 t/ha buckwheat pellets significantly reduced Canada thistle [*Cirsium arvense* (L.) Scop.], quackgrass, barnyardgrass and monochoria emergence in field rice, but did not affect the crop (234).

Weed suppression has also been reported with rice straw and rice residues. Several phenolics and momilactones contained in rice straw are presumed to synergistically contribute to the weed suppression (25,177). For example, rice flatsedge

(*Cyperus iria* L.) suppression in fields mulched (amended) with allelopathic rice residues and hulls was comparable with weed suppression resulting from a herbicide application (123). In another study, residues of an allelopathic rice cultivar applied at 5t/ha and incorporated at a depth of 5 to 6 cm reduced the population density and biomass of junglegrass [*Echinochloa colona* (L.) Link], monarch redstem (*Ammannia baccifera* L.), *A. multiflora* (Roxb.) and gulf leaf-flower (*Phyllanthus fraternus* Webster) (105). Inhibition of several common weeds in Vietnam rice fields was reported by incorporation of residues of *Alocasia cucullata* (Lour.) G. Don, *Sophora japonica* L., hairy beggarticks (*Biden pilosa* L.) and Jerusalem artichoke (*Helianthus tuberosus* L.) (Table 2) (84, 106).

Table 2.. Effects of incorporation of plant residues in rice fields on weed control and crop yield as compared to a standard herbicide treatment.[1]

Species	Weed reduction (%)	Yield increase (%)
Ageratum conyzoides L.	81	21
Bidens pilosa L.	82	23
Blechnum orientale L.	75	23
Leucaena glauca (Lam.) de Wit	86	23
Morus alba L.	73	23
Tephrosia candela L.	92	23
Euphorbia hirta L.	88	23
Eupatorium cannabinum L.	76	23
Herbicide treatment	78	12

[1]Modified from Hong *et al.* (84); [2]Pyributicarb (5 L/ha) and butachlor (600g/L)

Incorporation of plant residues produces considerable weed suppression that can lower crop production cost and reduce degradation of the environment. Further research efforts are needed to discover local plants that effectively suppress weeds. Foley (56) suggested that breeding/genetic manipulation can enhance the weed suppressive capacity of cover crops. It is feasible to transfer gene/genes responsible for synthesis of allelochemicals to desirable crop cultivars.

2.1.8. Microbes: In addition to the use of allelopathic crops, cover crops and residues to control or suppress weeds, the use of rhizobacteria and plant pathogens in weed management has received attention. Several reviews on using rhizobacteria and plant pathogens as bioherbicides are available (81,98,99,204). A few examples of successful weed suppression by rhizobacteria and plant pathogens are presented below.

2.1.8.1. Rhizobacteria: The downy brome, a common grass weed in wheat, causes an estimated $300 M annual loss in crop yields. Of more than 1000 pseudomonad isolates tested from winter wheat and the downy brome rhizoplane only two isolates suppressed the downy brome population (31%) and growth (53%) compared to the control with a concomitant 18 to 35% yield increase (97). In a controlled environment, the greatest downy brome suppression was found at cool (10 to 18 °C) and moist conditions (93). The downy brome is a cool season annual weed and establishes in wet autumn. Field application of the bacterium in autumn should result in biocontrol of the weed. Soil applied *Pseudomonas fluorescens* (strain D7) and *Ps. syringae* (strain 2V19) in naturally infested wheat fields suppressed weed growth by 25% and enhanced yield by 27% (96). An active principle isolated from cell-free or whole broth of *Ps. fluorescens* (strain D7) completely inhibited the downy brome at a concentration of 1 mg total dry wt/L agar. Analysis showed the active principle consisted of chromopeptides and other peptides, fatty acid esters, and a lipopolysaccharide matrix. However, separation of the components resulted in complete loss of inhibitory effect (75). Gealy *et al.* (64) reported that metabolites of *Ps. syringae* (strain 3366), grown aerobically as shake culture, inhibited the downy brome and 10 other plant species tested in soil and under field conditions. A crude ethyl acetate extract of the culture significantly suppressed the downy brome seed germination and root and shoot growth, but had little effect on wheat germination or growth. Analyses of the ethyl acetate extract revealed phenazine-1-carboxylic acid, 2-amino phoxazone and 2-amino phenol. The phenazine-1-carboxylic acid, a major component of the extract, suppressed the downy brome root growth by 99% at 5.7 mg/L. The presence of these compounds in the soil was confirmed by thin-layer chromatography suggesting that weed suppression was due to the phytotoxins produced. The toxin produced in the culture broth of *Ps. syringae* might be a source for the development of a bioherbicide.

Kennedy *et al.* (98) tested the inhibitory effects of *Ps. fluorescens* (strain D7) using both plant-soil and agar plate bioassays on 42 selected monocot and dicot weeds common in western and mid-western U.S. Among the test plant species, including the downy brome accessions, tested using the plant-soil bioassay, *Ps. fluorescens* inhibited the germination and growth of most weed species, but had no effect on wheat. These results indicate that *Ps. fluorescens* D7 may have the potential as a bio-control agent for the downy brome grass without any effect on non-target species.

Strains of *Ps. putida* (FH 160), *Stenotrophomonas maltophilia* (FH 131) and *Enterobacter taylorae* (FH 650) suppress the downy brome in wheat fields. The method of application of rhizobacterial biocontrol agent is an important consideration to consistently obtain effective weed suppression. Of the three methods tested, soil incorporation of inoculants into the soil profile at a depth of 10 to 15 cm produced consistent and significant weed suppression, diminishing its competitive ability than wheat seed treatment with inoculants or their soil surface application (137). Soil incorporation of bacteria produced consistent colonization of weed rhizosphere. The authors also suggested that incorporation of inoculants 10 to 15 days before the crop sowing would provide more effective weed suppression.

Field emergence of green foxtail [*Setaria viridis* (L.) Beauv.], a common world-wide weed, was suppressed with a granulated 'pesta' formulation (oat flour and maltose; 20% wt/wt) of *Ps. fluorescens* (strain BRG 100) (42). The 'pesta' product containing the bacterium was made into granules and had a shelf-life of 32 days. In field study, this product containing the pathogen suppressed the emergence of green foxtail by 90% over an 8-weeks period.

2.1.8.2. Pathogens: Besides rhizobacteria or their active component(s), pathogens also provide weeds control. For example, woollyleaf brusage [*Ambrosia grayi* (A. Neis.) Shinners] can be controlled by *Ps. syringae* pv. *tagetis* (195). An inundative single application of pathogen at a minimum of 10^4 colony forming units/ml in field tests produced sufficient disease symptoms (systemic chlorosis) to suppress the weed. An application of the pathogen in April, May or June was effective in suppressing the weed, but an application in July and August was not. The weed density was lower if applied in April than in May or June. It was suggested that the pathogen be used with herbicide to reduce the amount of chemical needed for weed control.

Ps. syringae pv. *tagetis* is also a pathogen of Canada thistle, a perennial weed that is difficult to control in soybean. Of the three application methods tested, an important consideration in delivering the bioagent under field conditions, a backpack sprayer was found to be the best method to apply the organism (72). Two applications [(each of 700 L/ha) of the inoculant containing 10^9 colony forming unit/ml plus Silwet L-77 (0.3% v/v)] provided a 67% increase in disease incidence (apical chlorosis) 4 weeks after treatment. There was an 81% reduction in flower buds and 20% reduction in shoot survival in the first year, but no effective weed control was observed in the second year. Silwet L-77, an organosilicone surfactant was required to facilitate *Ps. syringae* penetration into the leaf. A control method that only provides reduction in seed production is not an acceptable strategy for biocontrol of Canada thistle. The authors suggested that multiple inundative applications beginning when plants are young could be an effective control strategy. Another suggestion was enhancement of tagetoxin production, which is the primary compound causing the disease and blocking chloroplast biogenesis in developing leaves.

As shown in the previous example, the leaf wetness has a great effect on the efficacy of a pathogen used as a biocontrol agent. A wet or dew period is often required after application to insure fungal spore germination and penetration into the host plant cell. Tichich *et al.* (206) showed that the inoculum application during a wet period produced a greater population of bacterial cells inside the Canada thistle leaves than when the application was made during a dry period. As indicated by Auld *et al.* (11) product formulation is a constraint in the commercial development of many potential bioherbicides due to the fungi's dependency on dew or wet conditions limits their efficacy under dry conditions.

The potential of cyanogenic pseudomonads for weed suppression has been indicated by several authors. Pseudomonads (common rhizobacteria) are known for their ability to produce HCN, but the quantity produced varies widely (trace to >30 η moles/mg cellular protein) among species and strains of the bacterium. Significant growth inhibition (77 to 85%) of roots of lettuce (*Lactuca sativa* L.) and barnyardgrass by selected strains of *Ps. fluorescens* and *Pseudomonas* sp. was demonstrated (115). HCN evolved at less than 5 η moles/mg cellular protein is ineffective in inhibition of seedling growth. Selected cyanogenic pseudomonads applied inundatively to fields have potential to inhibit weed seedling emergence and growth, which would reduce weed competition and minimize the herbicide application. Rhizobacteria can also be manipulated to increase HCN production by addition of glycine (a precursor of HCN) to the soil.

Scentless chamomile (*Matricaria perforata* Merat), a pernicious weed in western Canada, is difficult to control because of its natural high tolerance to commercial herbicides. *Colletotrichum truncatum* (Schwein) is a host specific plant pathogen of the weed. A broadcast application of the pathogen at 200 L/ha containing a minimum of 50 X 10^6 spores/ml and at a dew point of 20 to 25 °C was reported to be conducive to develop infection and disease development resulting in significant weed suppression (69). However, a dew point of 20 to 25 °C is uncommon in the western Canadian prairie.

Therefore, it was concluded that the pathogen could be used as a component in integrated weed management, supplemented with a herbicide at a reduced dose or cultural/ mechanical control measures.

Chin (35) found that the fungal pathogens *Exserohilum monocerus* and *Cochliobolus lunatus* were effective for controlling barnyardgrass; an application of the fungi completely suppressed barnyardgrass emergence in the rice fields. Similarly, Thi *et al.* (205) reported that the fungal pathogen *Setosphaeria rostrata* was effective in suppressing Chinese sprangletop [*Leptochloa chinensis* (L.) Nees], which is a common weed in Vietnam rice production. A spray of the fungal spores at 10^6 / mL within 7 to 21 days after sowing the crop almost completely suppressed the weed.

Commercial products are being developed for three cosmopolitan weeds. Ragweed partheium (*Parthenium hysterophorus* L.), is highly invasive and a difficult weed to control in pastures and cultivated fields in India, Australia and other regions. A fungal pathogen *Puccinia melampodium* has excellent potential as a bioherbicide for the weed and it is being further tested by CAB Bioscience (Ascot center), U. K. (192). Barnyardgrass is a serious weed of world wide occurrence. Gohbara (68) reported that the fungal pathogen *E. monoceras* has potential to be marketed in Japan as a bioherbicide for barnyardgrass control in rice fields. This fungus is also used in China and Vietnam, while *Colletotrichum graminicola* is used in South Korea for barnyardgrass control. *Xanthomonas campestris* (trade name "Camperico") is marketed for annual bluegrass control (*Poa annua* L.) in golf courses in Japan. Another area where allelopathy has been successfully used is in the control of parasitic plants, where non-host plants are used to stimulate seed germination, or germination stimulants are applied to the soil.

2.1.9 Parasitic Weeds: Trap crops are an easy and effective method to control parasitic plants as *Striga*, *Orobanche*, *Cuscuta* and *Alectra*. Another strategy is to use catch crop that stimulates the germination of parasitic plant seeds and subsequently become parasitized. The parasitized plants are then destroyed. *Orobanche* and *Cuscuta* are problem parasitic plants in much of South-Central Asia and the sowing of a mixture of trap and catch crop seeds is a recommended strategy for their control (36, 168). Other control methods are based on adding germination stimulants to the soil.

Striga produces large numbers of seeds and chemical control of these plants is ineffective because their seeds remain dormant in the soil for several years. An attractive control strategy is application of chemical stimulant e.g. strigol to the field prior to sowing the crop in order to induce the parasitic seeds to germinate -- "suicidal germination" -- in the absence of a host (133). Another method is to inject ethylene gas into the soil as a germination stimulant. This is an excellent method of control, successfully used in the USA, but ethylene gas injection is expensive and hazardous and may not be suitable in developing countries. Three strains of *Ps. syringae* pv. *glycinea* are reported to synthesize large amounts of ethylene gas and are effective in promoting seed germination of several species of *Striga* (20).

Another strategy is to reduce germination of the parasitic weed seeds. Yonli *et al.* (239) found that 14 indigenous *Fusarium* isolates reduced seed germination of *Striga hermonthica* that causes severe damage to sorghum crops. The *Fusarium* isolates were grown either on sorghum compost or sorghum chopped straw and the inoculum was soil incorporated to a 5 or 10 cm depth. The isolates grown on compost substrate were more effective in reducing *Striga* seed germination, biomass and vigour than those grown on chopped straw substrate. In addition, the inoculum applied at the 5 cm depth was more effective than at 10 cm depth; all the isolates were effective in controlling *Striga*.

Several fungal plant pathogens have been found suitable as bioherbicide agents against important weeds. Examples of commercial mycoherbicides are 'Devine' containing *Phytophthora palmivora* for strangler vine [*Morrenia odorata* (Hook and Arn.) Lindlo.] control in citrus (102,179); 'Collego' containing *Colletotrichum gloeosporioides* f. sp. *aeschynomene* causing anthracnose to control northern jointvetch [*Aeschynomene virginica* (L.)] in rice and soybean [*Glycine max* (L.) Merr.] (28,196); and 'BioMal' containing *C. gloeosporioides* f.sp. *malvae gloeosporioides* for round-leaved mallow (*Malva pusilla* Sm.) control in small grains and lentils (128). These examples and those given in Table 3 indicate the potential of mycoherbicides.

Table 3. Fungal plant pathogens with the potential for common weed suppression.

Weed	Pathogen	Reference
Common lambsquarters (*Chenopodium album* L.)	*Ascochyta caulina*	187
	Cercospora chenopodii	
	C. dubia	
Giant ragweed (*Ambrosia trifida* L.)	*F. lateritium*	9
Johnsongrass (*Sorghum halepense*)	*Sphacelotheca holci*	134
Knapweed (*Centaurea diffusa* Lam.)	*Puccinia jaceae*	223
Large crabgrass [*Digitaria sanguinalis* (L.) Scop.]	*Pycularia grisea*	9
Prickly sida (*Sida spinosa*)	*Fusarium lateritium*	220
Purple nutsedge (*Cyperus rotundus* L.)	*Phyllachora cyperi*	9
Roundleaf mallow (*Malva pusilla*)	*C. gloeosporioides*	144
Skeleton weed (*Chondrillina juncea*)	*Puccinia chondrillina*	77
Velvetleaf (*Abutilon theophrasti*)	*Colletotrichum coccodes*	82
Water hyacinth [*Eichornia crassipes* (Mart.) Solms]	*Cercospora rodmanii*	39
	Alternaria eichorniae	147

2.2. Diseases

2.2.1. Allelopathic crop plants: Allelopathic crops not only can be used in weed control, but also their leachates, exudates and residues inhibits the plant pathogens i.e. to control plant diseases. For example, Ramirez-Villapudua and Munneche (169) reported that dried cabbage (*Brassica oleracea* L. var. *capitata*) incorporated into the soil significantly reduced the yellow cabbage pathogen (*F. oxysporum* sp. *conglutinan*) population and produced near disease-free cabbage plants. Methanethiol, dimethyl sulfide and dimethyl disulfide from the residues were suggested to have contributed to disease suppression. Dried residues of cruciferous plants (cabbage, mustard and turnip [*Brassica septiceps* (L.H. Bailey)] as mulch significantly reduced the root rot pathogen (*Aphanomyces euteiches*) in peas (160). Reeleder *et al.* (172) reported that a combination of white pine (*Pinus strobes* L.) and red pine (*P. resinosa* Aiton) bark mulch suppressed the damping-off caused by (*Rhizoctonia solani*) in ginseng (*Panax quinquefolius* L.) under field conditions. White pine bark mulch also reduced the weed population in the early stages, improved root shape and supported larger plant population of ginseng crop compared with commonly used oat mulch. Cedar (*Cryptomeria japonica* D. Don.) and Hinoki cypress (*Chamaecyparis obtuse* Endl.) barks decompose very slowly in the field and therefore, are unsuitable as mulch. However, the Chinese use the bark fibres for raising seedlings in the green house, and no soil borne root disease was found (241). The fibers contain essential oils soluble in ethanol that inhibits *Ps. solanacearum*, *F. oxysporum,* and *F. lycopersicum* growth, which suggests that these compounds contribute to disease control (241).

2.2.2 Microorganisms/rhizobacteria: Increased interest in microorganisms as safe and effective agents for plant disease control is evident from the number of books, reviews and symposia (34,95,185,219,225). An example of a biofungicide based on *Streptomyces* sp. is "Mycostop." Developed in Finland (1990) it is registered in USA and several eastern European countries as biofungicide against damping-off diseases (*F. oxysporum* and *R. solani*) and partial control of grey mold (*Botrytis cinerea*) infection of strawberry (*Fragaria* L.) flower. Recommended methods of application are seed treatment, drenching the substrate and drip irrigation (142,143).

The concept of using rhizobacteria as biocontrol agents for plant disease control was first demonstrated by Kerr (103) who showed that peach seeds inoculated with *Agrobacterium radiobacter* var. *radiobacter* (strain 84) significantly suppressed the peach [*Prunus persica* (L.) Batsch] crown gall in soil infested with the crown gall pathogen *A. radiobacter* var. *tumefaciens*. This was the first bacterium used as a biocontrol agent to control a specific plant disease, as well as the first commercially produced bacterial agent for plant disease control (104). The disease control mechanism was suggested to be due to the production of a new kind of antibiotic (nucleotide bacteriocins) that selectively inhibits most pathogenic agrobacteria.

2.2.2.1 Crop production: Wheat seeds inoculated with *Ps. fluorescens* (strain13-79) suppressed 'take-all' pathogen (*Gaeumanomyces graminis var. tritici*) of wheat in naturally infested field soil. Fewer plants in the inoculated fields developed foliar symptoms of disease and showed less root infection resulting in 27% wheat yield increase. Wheat 'take-all' suppression was suggested to be related to increased level of 2,4-diacetylphloroglucinol or phenazine-1-carboxylate produced by the introduced inoculants (226). *Ps. fluorescens* (strain 2-79) was inhibitory *in vitro* to wheat take-all (76,226,227). *Ps. corrugata* (strain 2140) also suppresses the wheat take-all (*G. graminis* var. *tritici*) *in vivo* at 15 °C and inhibits the pathogen *in vitro* in the range of 10 to 15 °C (184).

Wen-Hua *et al.* (228), after screening hundreds of bacterial isolates, found that a strain of *Bacillus subtilis* (B-908) was antagonistic to *R. solani* that causes rice sheath blight disease. There was no lodging of rice plants in field plots treated with the strain B-908, compared to severe lodging in untreated plots. The same isolate also suppressed the 'sharp eye spot' on wheat seedlings caused by *R. cerealis* in pot experiments.

Cotton seeds treated with *Ps. fluorescens* (pf-5) suppressed cotton damping-off and root rot caused by *Pythium ultimum* and/or *R. solani*; pyoluteorin and pyrrolnitrin were demonstrated to be antibiotics involved in the disease suppression (85,86). In field experiments, Reddy *et al.* (170) reported that two *Ps. fluorescens* strains (63-49 and U-14) consistently and effectively suppressed the damping-off caused by *R. solani* in canola, when seeds were treated with either a peat-based or liquid inoculant before planting.

While testing bacterial strains of *Ps. fluorescens* and *Bacillus* spp. against damping-off (*R. solani*) on the common bean (*Phaseolus* L.), Andrade *et al.* (8) found that *Bacillus* sp. (strain P183) was highly effective in suppressing the disease under field conditions and produced better control than a fungicide treatment (quintozene).

2.2.2.2 Forestry: Fungal root disease causes considerable damage in conifer nurseries and on reforestation sites. Out of the 500 isolates tested, Reddy *et al.* (171) reported that application of *Burkholderia cepacia* (strain RAL3) and *Ps. fluorescens* (strain 64-3) reduced the root disease in white spruce [*Picea glauca* (Moench) Voss] seedlings caused by *F. oxysporum.* This organism also improved the seedlings health when seedlings were planted in soil contaminated with *Fusarium sp.* and *Pythium sp.* in a nursery situation, as well as improved the survival of bare roots white spruce seedlings planted in reforestation sites. The conifer seeds were inoculated with the bacterial suspension in a liquid formulation. Both strains were consistently effective as biocontrol agents in reforestation trials, and strain RAL3 maintained acceptable population density for a year when its commercial formulation was stored at 5 °C. A total of 25 microorganisms have been registered with the U.S. Environmental Protection Agency as biopesticides against plant diseases (57). Other examples of rhizobacteria that exhibit disease control traits are presented in Table 4.

Table 4. Other examples of rhizobacteria with potential to control root disease

Rhizobacteria	Pathogen	Host	Reference
Arthrobacter sp.	*Fusarium oxysporum*	Carnation	197
Serratia liquefaciens	*F. oxysporum*	Carnation	198
Hafnia alvei	*F. oxysporum*	Carnation	198
Bacillus sp.	*Gaeumanomyces graminis*	Wheat	30
Pseudomonas sp.	*Erwinia carotovora*	Potato	174
Ps. fluorescens	*F. oxysporum*	Radish	121
Ps. fluorescens	*Ps. syringae* pv. *phaseoli*	Bean	4
Ps. fluorescens	*Ps. syringae* pv. *pisi*	Pea	5
Ps. fluorescens	*R. solani*, *Py. ultimum*	Cucumber	238
Ps. putida	*Colletotrichum orbiculare*	Cucumber	125
Ps. cepacia	*R. solani*	Cotton	163
B. subtilis	*R. solani*	Cotton	71
Burkholderia cepacia	*F. oxysporum*	Corn	21
Rhizobacteria	Bacterial blight	Rice	216
Bacillus sp.	*Phytophthora cactorum*	Apple	74

2.2.3 Induced resistance: Research over the last two and half decades indicates that plants possess latent defensive mechanisms that become activated following exposure to live/killed microbes (18,201). This immunization or induction of systemic disease resistance (ISR) was first reported by Scheffer (188) when he observed that prior inoculation of elm (*Elmus* L.) trees with four selected fluorescent pseudomonads led to significant reduction in systemic foliar Dutch elm disease (*Ophiostoma ulmi*). Induced systemic resistance has been reported in > 25 crops (116,212). The biochemical changes after stress are accumulation of chitinases, glucanases, peroxidases, phytoalexins (138,213).

Wei, Kloepper and Tuzun (224) demonstrated that cucumber seeds inoculated with *Ps. putida* (strain 89B-61), *Serratia marcescens* (strain 90-166) and *Flavomonas oryzihabitans* (strain INR-5) induced resistance against 'angular leaf spot' (pathogen = *Ps. syringae* pv. *lachryman*) and anthracnose (pathogen = *Colletotrichum orbiculare*). All three rhizobacterial strains significantly reduced the foliar lesion diameter. Two strains (89B-61 and 90-166) significantly increased the cucumber yield over the control. Application of selected strains of *Ps. putida* and *S. marcescens* induced the resistance against fusarium wilt in cucumber (125). Increased level of phytoalexin was reported in carnation, inoculated with *Pseudomonas sp*. (strain WCS 417s), which induced resistance against root rot by *F. oxysporum* (214).

Similarly, Duijff *et al.* (48) reported seed inoculation with *Ps. putida* (strain WCS358r) significantly reduced the fusarium wilt in carnation (*Dianthus caryophyllus* L.) caused by *F. oxysporum* f. sp. Dianth. In this case, siderophore (iron chelating enzymes) mediated competition for iron was suggested as the mechanism of disease suppression. Siderophore producing rhizobacteria can bind most of the available iron in the rhizosphere preventing pathogens from proliferation due to lack of nutrient (151). A mutant strain of *Ps. putida* that over-produces siderophores was more effective to control tomato (*Solanum lycopersicum* L.) root rot caused by *F. oxysporum* than wild *Ps. putida*.

Hynes and Lazarovits (87) recorded a higher level of PR-(pathogen related) protein in bean and tomato leaves following seed treatment with a rhizobacterium. Increased peroxidase activity of root surface (3), and lignification of stems/leaves in bean (7) and potato (59) have been recorded following root colonization by rhizobacteria. These reports indicate that root/seed colonization by rhizobacteria elicits physiological changes resulting in ISR in host plants.

Fusaric acid is a common compound in *Fusarium* infection and its ability to hydrolyze the acid is the mechanism that regulates the infection in several plants (209). Several rhizobacteria, as *Ps. cepacia* and *Ps. solanicearum*, are capable of hydrolyzing fusaric acid. Frindlender *et al.* (58) reported that 1,3 glucanase from a strain of *Ps. cepacia* damaged the fungal mycelia and also effectively reduced the disease onset by *R. solani*, *Sclerotium rolfsii* and *Pythium ultimum*. A genetically manipulated strain of *Ps. fluorescens* that produces pyoluteorin and 2,4-diacetylphloroglucinol effectively protects the cucumber plants against *Pythium ultimum* infection (189). Voisard *et al.* (217) demonstrated that *Ps. fluorescens* (strain CHAO) inoculation could suppress tobacco (*Nicotiana* L.) black root rot (pathogen = *Thielaviopsis basicola*); disease resistance was associated with increased HCN production. Asparagus (*Asparagus officinalis* L.) root growth increased 30% in controlled conditions when 3 week-old seedlings were dipped in culture filtrate of *Ps. putida* isolated from asparagus rhizosphere (240). The isolate was antagonistic to *F. moniliforme* and the active principle in the filtrate was a mixture (45:55) of succinic and lactic acids. Seedlings treatment with 1:1 mixture of acids at 10 ppm enhanced the root growth upto 40%. The authors suggested that beneficial effect of some rhizobacteria might be due to secretion of organic acids, and that these acids might reduce pathogen population density resulting in plant growth promotion. Kumar and Dube (117) reported that bacterization of chick pea (*Cicer arietinum* L.) and soybean seeds with fluorescent *Pseudomonas* sp. (siderophore producing, isolated from tomato rhizosphere) increased the seed germination, growth and yield of both plants. Inoculation of chick pea reduced the wilt disease by 52% in wilt-sick soil. Potato seed pieces inoculation with selected strains of *Ps. fluorescens* and *Ps. putida* enhanced the potato yield and it was suggested that the yield increase was due to suppression of HCN producing microbes by the introduced inoculants (112).

Disease suppression invariably enhances the host plants growth and yield. It is neither necessary nor even desirable to try to distinguish between plant growth promoting and disease suppressing rhizobacteria. Although ISR has been demonstrated in several crop plants under field conditions, its application in agriculture has not materialized because of lack of technology development.

3. PLANT GROWTH PROMOTION

3.1 Crop growth stimulation by companion crops/plants: Allelopathic growth stimulation of crops by plants is under-investigated and only a few examples are cited here. Corn cockle (*Agrostemma githago* L.) stimulation of wheat growth and yield was reported from former Yugoslavia in 1960's (62). The growth factor involved was identified as agrostemin, consisting of principal component allantoin, several amino acids and purines, and was given a commercial patent. Soil amended with alfalfa residues stimulated the tomato, cucumber, lettuce growth in greenhouse experiments and the growth factor was identified as triacontanol, a primary alcohol (180). Foliar application of allelochemical stimulated the rice, corn and barley growth. In a simple experiment using a U-tube, Rice (176) demonstrated that ground ivy (*Glechoma hederaceae* L.) stimulated the radish (*Raphanus sativa* L.) growth. Mallik and Watson (132) reported that the incorporation of black nightshade (*Solanum nigrum* L.) residues stimulated the soybean growth and nodulation in pot experiments (Figure 1).

3.2 Crop growth stimulation by rhizobacteria: Rhizobacterial growth promotion is mediated directly by the production of growth regulators (10), and indirectly by controlling plant pathogens, facilitating mineral uptake, promoting mycorrhizal fungal growth, enhancing biological nitrogen fixation (BNF) (symbiotic and diazotrophic) and suppressing the debilitating rhizobacteria (DRB). Growth promotion is most often host cultivar specific (19,38,162). Several abiotic and biotic factors influence the rhizobacterial growth promotional function (200). Production of growth regulators by rhizobacteria plays important role in plant growth promotion.

Glick *et al.* (67) reported that canola seed inoculated with *Ps. putida* (strain Gr 12-2) promoted early seedling emergence, root and shoot growth under stressed soil and temperature conditions compared with a mutant strain lacking the enzyme ACC deaminase. Twelve strains of *Bacillus* sp., isolated from spring wheat rhizosphere, were tested for their growth promotional potential of wheat cultivars at eight sites with different soil types (Saskatchewan, Canada) over three years. Eight of the *Bacillus* strains increased tiller numbers irrespective of locations or years, one isolate increased the wheat yield at two locations in two of the three year study (70). Another isolate increased yield by 2 to 12 % at three of the five locations during the study (70).

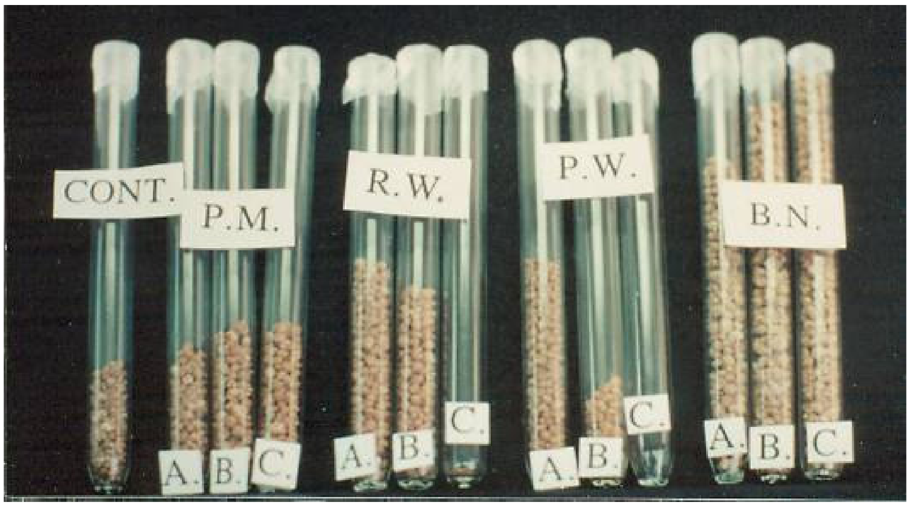

Figure 1. The effects of peat moss (PM), giant ragweed (RW), redroot pigweed (PW) and black nightshade (BN) at 2.5 (A), 5.0 (B) and 10.0 (C) mg of residue/g of sand on soybean nodulation. Control was sand only. From Mallik and Watson (132).

After several years of field testing, Backman *et al.* (12) reported that *B. subtilis* strain A-13 and GB03 in combination with a fungicide significantly promoted the growth of pea and suppressed *Rhizoctonia* and *Fusarium* spp. that cause root disease. The isolate is a promiscuous inoculator of both monocots and dicots, is a spore former and highly tolerant to environmental and soil stresses. The strain GB03 together with GB07 has been commercially introduced (trade name "Quantum") for its growth promotional effect. *Ps. cepacia* (strain PCI) suppressed the phytophthora blight (*Phytophthora capsici*) and enhanced the growth and yield of red pepper (107). However, the results were inconsistent depending on the year and location. The antibiotics cepacid from the strain PCI and pseudane A from the strain PCII (another strain of the same bacterium) completely suppressed the pathogen *in vitro*. Seeds (previously coated with methoxy cellulose and "celite") treated with pseudane A [2-(2-heptenyl)-3methyl-4-quinolinone] increased the fresh weight (40-76%) and plant height (16-22%), and the authors suggested that growth stimulation was due to antibiotic pseudane A (107).

Seeds inoculated with pseudomonads improved the soybean and canola (110) seedling emergence in the field, but the mechanism of germination promotion is unclear. Rice and cotton seeds inoculated with *Ps. fluorescens* biotypes C and G increased plant growth and inhibited several plant pathogens (*F. oxysporum*, *R. solani*, *Acrocylindrium oryzae*, *Xanthomonas campestris*, and *Ps. syringae*) (186). Presumably the growth promotion was due to disease suppression. Gupta *et al.* (73) reported that peanut seed inoculated with fluorescent *Pseudomonas sp*. (GRC2), which produces siderophores, HCN and IAA, significantly enhanced seed germination, early seedling growth, nodule weight, crop yield and suppressed the charcoal rot disease (*Macrophomina phaseoli*) when planted in pathogen-infested soil. Here the pathogen suppression played a prominent role in growth promotion, while the siderophore, HCN and IAA production contributed to growth enhancement. Potato seed tubers treated with fluorescent pseudomonads (strains WCS 365, 358, 374) increased potato yields by 70% than control (65). These siderophore strains producers, were more effective than inhibitory substance producers. For additional examples of growth promotion by rhizobacteria see Table 5.

Table 5. Additional examples of growth promoting rhizobacteria.

Crop	Rhizobacteria	Reference
Barley	*Pseudomonas* sp.	90
Bean	*Ps. putida*	7
Canola	Rhizobacteria	108, 109
Corn	*Pseudomonas* sp.	83
Corn	Rhizobacteria	90
Cotton	*B. subtilis*	13
Lentil	*Ps. putida* (G 2-8; G 11-32)	31
Cabbage	*Ps. aeroginosa*	66
Onion	*Ps. fluorescens*	66
Peanut	*B. subtilis*	211
Potato	*Ps. fluorescens*, *Ps. putida*	218
Radish	Rhizobacteria	111
Tobacco	*Azotobacter*	183
Vegetables	Rhizobacteria	52
Wheat, spring	*Bacillus* sp.	32
Wheat	*Azorhizobium caulinodans*	135

3.3 Biofertilizers: Biofertilizers have recently gained attention as a consequence of public desire for organic food. Application of biofertilizer or microbial inoculant as a supplement to chemical fertilizers reduces crop production cost, improves soil properties and promotes soil–microbial balance. Depending on the nutritional status of the soil and the crop being cultivated, a possible composition of a bio-fertilizer might include: (i) biological nitrogen fixer (BNF) - symbiotic, and/or associative, endophytic diazotrophs, (ii) P- and K-solubilizing bacteria, (iii) growth-promoting rhizobacteria (pseudomonads and/or others), (iv) biocontrol agents against soil-borne pathogens, (v) bioherbicides, (vi) VAM fungi and (vii) nematode-trapping fungi (153, 208).

Adequate nitrogen availability is a key element in crop production, and the availability of an adequate carbon source in the rhizosphere is a major factor in the nitrogenous activity. The potential of endophytic and associative diazotrophs as contributors to the nitrogen pool in agricultural fields and in pastures has been recognized. Genera of diazotrophs of agricultural importance include *Azospirillum*, *Azotobacter*, *Acetobacter*, *Burkholderia*, *Herbaspirillum*, *Spirillum*, *Closrtidium,* as well as a few genera belonging to Enterobacteriaceae.

Root inoculation of *Azospirillum* stimulates proliferation of lateral roots and root hairs (94, 207), which promotes phytohormone production, uptake of nitrogen (55) and minerals (124), as well as production of antifungal and antibacterial compounds (53, 155, 159). Insoluble phosphate compounds are not available to plants. Phosphate-solubilizing rhizobacteria (selected species of *Bacillus*, *Flavobacterium*, *Micrococcus*, *Mycobacterium* and *Pseudomonas*) are reported to stimulate root activities, increasing organic acid secretion from roots, thus assisting phosphate-solubilization and promoting plant-mycorrhizal symbiotic association furthering phosphorous uptake.

3.3.1 Rice: Soil application or seed inoculation of *Azospirillum lipoferum* in field experiments resulted in a 22 % increase in rice grain yield (15) and enhanced the uptake of P and ammonia (145). Islam and Bora (89) reported that *A. lipoferum* inoculation reduced the bacterial leaf blight resulting in growth promotion and yield. Mirza *et al.* (140) reported that *Herbaspirillum* can contribute 19 to 58% nitrogen needs of rice crop depending on crop cultivar and bacterial strain used. Inoculation of rice seedlings with *Burkholderia vietnamiensis*, an isolate from the rhizosphere of young rice plants significantly enhanced rice grain yield (0.8 t/h) in field experiments (210). An endophytic species of *Burkholderia* isolated in Brazil can fix 31% of the nitrogen required by the rice plant and its application increased the plant biomass by 69% under gnotobiotic conditions (16).

Azotobacter chroococcum and *A. vinelandii* have been used in the majority of the studies. Application of *Azotobacter* is reported to increase rice yields by 20% (236). Although reports of growth promotion by *Azotobacter* application abound in the literature, inconsistent results are reported as well.

Clostridium, an obligate anaerobe, can fix nitrogen only in presence of a high level of utilizable carbon. The inoculants can significantly enhance rice yield by returning straw to the field raising the carbon to nitrogen ratio (141).

Diazotrophic rhizobacteria commonly occurring in rice include *Azospirillum*, *Herbaspirillum* and *Burkholderia* (16, 129). These diazotrophs, including cyanobacteria, can substantially contribute to nitrogen requirements of rice plants under favorable soil conditions for nif-genes function. Based on extensive studies at IRRI, Watanabe *et al.* (222) and Rogers and Ladha (182) concluded that BNF can provide up to 25% of nitrogen requirements of rice plants in the field. Yanni *et al.* (237) and Biswas *et al.* (22,23) reported significant rice yield increases in a clover-rice rotation. They suggested that the rhizobia from clover improved utilization of available soil nutrients by improving rice root morphology and physiology, resulting in growth promotion and yield. Other examples of beneficial effects of plant-diazotroph associations are presented in Table 6. Although examples of beneficial effects of diazotrophs are replete in literature, inconsistency in expected results has impeded exploitation of the diazotrophs in agriculture. Principal reasons for this are (i) inadequate understanding of the complex interplay between the introduced inoculants and indigenous microflora in the rhizosphere and (ii) their response to edaphic and environmental factors.

The biofertilizer ("BioGrow") used in Vietnam consists of (i) *Ps. fluorescens*/*Ps. putida* (BNF), (ii) *Klebsiella pneumoniae* (anaerobic BNF, PO4-solubilizer) and (iii) *Citrobacter freundii* (BNF, antagonistic to 50% of common rice rhizospheric bacteria, but not to the two other components of the biofertilizer) (150). The inoculant is prepared by adding broth culture of bacteria separately in a carrier material made of clay soil (50%),

Table 6. Beneficial effects of plant-diazotroph associations on crop yield under field conditions

Crop	Diazotrophs	Yield increase (t/ha)	Reference
Sugarcane	*Azospirillum brasilense*	9 (cane)	193
	A. diazotrophicus	5 (cane)	193
Rice	*Azotobacter* sp.	0.9 (grain)	236
Corn	*Herbaspirillum seropedicae*	1.5 (grain)	181

Modified from Kennedy *et al.* (99)

rice husk (25%), sugar (1%) broth culture (24%) and water. The three inoculants thus prepared separately are mixed together in the field prior to application (10 parts each of 1 and 2, and 1 of 3). The bio-fertilizer is applied in the field by evenly hand spreading at 111 kg/ha. Non-inoculated carrier at 222 kg/ha served as control. The biofertilizer application significantly increased grain yield and nitrogen uptake (150) (Table 7). Biofertilizer containing two cyanobacteria (*Anabaena* and *Nostoc*), *Azospirillum* sp. and *Azotobacter* sp. field applied, along with 1/3 of the recommended amount of urea fertilizer for rice cultivation produced the greatest tiller number, harvest index, grain size and yield than any other treatment combinations of biofertilizer components and nitrogen fertilizer (236). Similar multi-strains biofertilizer are now being used in Australia (230), Pakistan (129) and Egypt (80). Overall rice grain yield increase is reported to be about 20%.

Table 7. Effects of farmyard manure and multi-strain biofertilizer on rice grain yields

Manure (kg/ha)	Biofertilizer (kg/ha)				
	0	111	222	444	Mean
		Grain yield (kg/ha)			
5560	5476	6170	5890	5801	5834
11120	5443	6360	6111	5979	5973
22240	5764	5813	6116	5854	5888
Mean[2]	5561b	6114a	6039a	5878a	

[1]Modified from Nguyen *et al.* (150); [2]Means followed by the same letter are not significantly different at the p=0.05 level as determined by LSD test.

3.3.2 Wheat: A variety of diazotrophs occur in wheat rhizosphere: *Azospirillum*, *Azotobacter*, *Azorhizobium*, *Bacillus*, *Herbaspirillum* and *Klebsiella*. A 30% increase in wheat yield was reported with *A. brasilense* under field conditions with low rates of nitrogen fertilizer (50 to 60 kg N/ha), while at higher nitrogen rates the effect of the organism was eliminated (155). The yield response varied depending on the wheat cultivar. Compatibility between the host cultivar and bacterial strain is highly desirable for maximum benefit of the association due to differences among the bacterial strains efficacy. Based on the evaluations of over 20 years of field applications of *A. brasilense* and *A. lipoferum*, Okon and Labandera-Gonzales (155) concluded that application of *Azospirillum* can increase crop growth and yield by 5 to 30% depending on soil and climate conditions.

Herbaspirillum, an endophytic diazotroph, colonizes wheat, rice, corn, sorghum, sugarcane (*Saccharum officinarum* L.) and other graminaceous plants. El-Mohandes (51) reported that application of *H. seropedicae* significantly increased straw and grain yields in wheat, as well as percent nitrogen recovery under field conditions. Earlier the same bacterium was also shown to enhance seed emergence (161). Other studies indicated that the application of diazotrophs (BNF) and/ PGPR can supplement fertilizer use in wheat cultivation (80,101,155), while Kennedy and Islam (100) found that wheat diazotrophs can contribute from 10 to 30 kg N/ha.

3.3.3 Cotton and corn: Cotton seedling root inoculated with *A. brasilense* enhanced the root and root hair growth resulting in significant nitrogen uptake (0.91 mg/N/PL), as well as an increase in plant height and dry matter (55). Inoculated plants were able to produce antifungal and antibacterial compounds, growth regulators and siderophores (159). *Azotobacter* inoculation increased the cotton yields up to 28% as than controls (88).

Corn requires large nitrogen inputs to maximize yields. Garcia de Salamone *et al.* (63) using ^{15}N dilution technique demonstrated that BNF contributes significantly to the nitrogen needs of the crop. Commonly found diazotrophs included *Enterobacter*, *Rahnella aquatilis*, *Paenibacillus*, *Azotofixans*, *Azospirillum*, *Herbaspirillum seropedicae*, *Bacillus circulans* and *Klebsiella* (33). Application of biofertilizer containing *A. brasilense* increased corn yields from 50 to 95% (0.7 to 1.0 t/ha) depending on soil nitrogen status, when the nitrogen fertilizer was applied at low to medium levels (18 to 46 kg/ha), but at higher rates of nitrogen fertilizer the inoculation effect was reduced. The amount of nitrogen fixed varies greatly between host cultivars and strains of *Azospirillum* used. The positive effect of the inoculant is mainly physiological improvement of the inoculated plants promoting nutrient and water uptake (154). As stated before, the bacterial strain and host cultivar play very important roles in the function of biofertilizer (44, 45).

Corn seed inoculation with *H. seropedicae* increased the corn grain yield in greenhouse experiments by 49 to 82% with applied nitrogen fertilizer, compared to 16% increase without fertilizer. These results indicate that the inoculum improved the nitrogen assimilation of plant. Application of inoculant in field experiments at different locations in the USA, with a uniform application of 224 kg N/ha at each location, increased the corn yield across locations by 21% (181) (Table 8). Seed inoculation with a selected strain of *Burkholderia cepacia* enhanced corn yield by 6.3% in field experiments, while under greenhouse conditions using non-sterile soil corn yield increased between 36 to 48%, depending on host cultivar and bacterial genotype (181). Beneficial effects of *Azospirillum lipoferum*, *A. indiegens* and *Azorhizobium caulinodans* inoculation were also reported by the same authors (181). The positive response of corn seed inoculation with *Rhizobium leguminosarum* bv. *trifolii* and *R. etli* may be interpreted as PGPR effects. As in other instances compatibility between genotypes of both the host and *Rhizobium* plays an important role in the function of the association.

The application of biofertilizer containing *A. chroococcum*, *B. megaterium* (P-solubilizer), *B. mucilaginous* (K-solubilizer) and *Glomus mosseae* or *G. intradices* (VAM fungus) under greenhouse conditions using garden soil enhanced the corn growth and plant height in 87 days pot experiments compared with no amendment, chemical (urea, KH_2PO_4, KCL) or organic (chicken manure with rock phosphate) fertilizers. The bio-fertilizer application also improved the soil properties and increased P and K uptake by the plants.

Table 8. Effects of rhizobacterial inoculants with a 224 kg/ha nitrogen application on corn yield at two locations in the U.S.

Location	Rhizobacteria	Yield (t/ha)[1]	Yield increase (%)
Lancaster	*Klebsiella pneumonia*	17	26
	Bacillus sp.	17	30
Arlington	*Pantoea agglomerans*	14	18
	H. seropedicae	15	12
	Klebsiella sp.	16	20

[1]All treatment yields are significantly different from their controls at p=0.05 or better. Modified from Riggs *et al.* (181)

The application of biofertilizer containing *G. mosseae* produced greater biomass, while biofertilizer with *G. intradices* increased the plant height (233). James *et al.* (91) reported earlier that *H. seropedicae* can also fix nitrogen in corn.

3.3.4. Sugarcane: Sugarcane, like corn, requires large inputs of nitrogen (193,194). Application of diazotrophic PGPR, as *Acetobacter* (*Gluconacetobacter*) and *Herbaspirillum*, significantly reduces the amount of nitrogen fertilizer needed (47). Boddey *et al.* (26), using ^{15}N natural abundance technique showed that BNF can contribute 60% of nitrogen assimilated by sugarcane not receiving nitrogen fertilizer. Considering the limit of the accuracy of the technique used, it is possible that a part of the nitrogen is assimilated from soil facilitated by PGPR effects of the inoculants. Dobereiner (46) concluded that BNF can contribute up to 150 kg N/ha. Muthukumarasamy *et al.* (146) reported that inoculation of sugarcane settes with biofertilizer (containing *Acetobacter diazotrophicus*, *A. lipoferum*, *Herbaspirillum* sp. and vesicular arbuscular mycorrhiza) in field experiments that received 50% recommended nitrogen fertilizer produced the same cane yield as that receiving only the recommended fertilizer rate (control). The authors suggested that the diazotrophs might have contributed a major quantity of plant nitrogen requirement. The bacteria also produced appreciable amounts of IAA that helped promote rooting and growth. They concluded that bio-fertilizer application could reduce nitrogen fertilizer application by 50% without loss in yield.

The diazotrophs commonly found in sugarcane roots and stems (rhizosphere, rhizoplane and also endophytically) include *Acetobacter diazotrophicus*, *A. brasilense*, *A. lipoferum*, *A. amazonense*, *Bacillus brasiliensis*, *Burkholderia tropicalis*, *Herbaspirillum seropedicae* and *H. rubrisubalbicans* (100,173,186,200). The endophytic diazotrophs colonize sugarcane spontaneously and their numbers decline where fertilizer nitrogen is used rendering the plant more dependent on fertilizer. *A. brasilense* and *A. lipoferum* occur in roots, stems and leaves of sugarcane. Soil application of bacteria is reported to enhance cane yield by 9 and 5 t/ha in the first and ratoon crops, respectively (194). *Acetobacter* (*Gluconacetobacter*) *diazotrophicus*, an endophytic acid tolerant biological N-fixer that grows best in sugar rich medium contributes from 60 to 80% of sugarcane plant nitrogen (equivalent to 200 kg N/ha) (27). Seedling inoculation with an effective strain of the bacterium has become part of commercial sugarcane cultivation (120). *H. seropedicae* and *H. rubrisubalbicans* occur endophytically in roots and stems of sugarcane. *H. seropedicae* can significantly enhance cane yield and leaf nitrogen content (146).

Application of fertilizer-N up to 300 kg N/ha does not reduce population density of the bacterium in field (173). Meyer *et al.* (139) reported that *Burkholderia brasiliensis* and *B. tropicalis*, endophytic in sugarcane roots and stems, are antagonistic to nematodes.

4. RHIZOBACTERIAL SELECTION AND PRESERVATION

Two criteria for the screening of rhizobacterial strains are the (i) selection of effective strains to suppress pests and/or promote growth of a compatible host and (ii) the ability of the strain to establish and maintain an effective population density throughout the lifecycle of the host plant (151). A standardized screening procedure is needed. Introduced inoculant bacteria must compete with indigenous microbes to colonize the host's rhizosphere. Rigorous testing for the strain's performance at different stages of the host's lifecycle in the field is necessary to select the most effective strain for potential commercial application.

Because the loss of selected traits through mutation is possible, preservation and maintenance of the selected rhizobacteria are important. Freezing-drying is the preferred method of preservation and maintenance of the bacterial culture. However, when freeze-drying facilities are unavailable, there are other acceptable methods available (132). After regeneration of the preserved bacterium, harvesting the cells in the late exponential growth phase for the inoculant preparation is recommended. Rigorous checking, as is done for rhizobial inoculants, of the inoculant bacteria for their original traits for which they were selected is needed to insure that they maintain their effectiveness. Preparation and production of the inoculant are discussed elsewhere (132).

5. CONCLUSIONS

Allelopathic research began in earnest in the early 1960's as an intellectual curiosity, but soon it was realized that its principle could be applicable for pest management in low input agriculture. Low input agriculture utilizes all available natural resources for pest management. Research of the past half a century has made the concept feasible. Efforts to identify allelopathic crop accessions and the plants whose residues indicate weed suppressive potential should be accelerated. Selection of rhizobacteria for plant growth promotion and weed and plant pathogen suppression deserves emphasis. Often ignored is the compatibility of selected rhizobacterium with the host plant and its competitiveness with the indigenous microbes in the host's rhizosphere. Substantive progress has been made in identification of allelochemicals; more effort is needed in this area. Identification of the gene(s) related to allelochemical production or other desirable traits should receive more attention. Rhizobacterial application demonstrated positive results of weed and plant pathogen suppression, as well as plant growth promotion, but inconsistencies between the laboratory and field results impede their use in farming systems. A better understanding of microbial ecology in the host rhizosphere and its interaction with the introduced inoculant can reduce this inconsistency leading to increased application of rhizobacterial inoculant in low input farming systems. Application of wild or genetically manipulated rhizobacteria is likely to increase in the future as a component of sustainable agriculture.

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