Recent Advances in the Biological Control of Soil-Borne Pests and Pathogens

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Abstract

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In general, two approaches have been followed to achieve biological control of soil-borne pests and pathogens: i) enhancement of the natural potential of suppression that exists in every soil, and ii) introduction of a natural or improved efficient strain of antagonistic microorganism. Both approaches need a good knowledge of the biology and ecology of target organisms and biological control agents. The natural or introduced population of antagonists must be target-specific, present and active at a place and a time at which the pathogen is susceptible to its antagonistic activity. Significant advancement has been made in biochemical and molecular approaches to understand the modes of action of several biological control agents such as *Trichoderma* spp., fluorescent pseudomonads, nonpathogenic *Fusarium oxysporum*, etc... knowledge of the modes of action is required to: i) improve the methods of screening of potential biological control agents, ii) choose strains having different modes of action to be used in mixtures, iii) select the best conditions to produce, formulate and apply the biological control agents. For instance, the association of a nonpathogenic strain of *F. oxysporum* competing with the pathogen for carbon with a strain of fluorescent *Pseudomonas* competing for iron always improved control of fusarium wilt in tomato and carnation. To improve the long-term effect of this control, it would be interesting to add a third strain of either nonpathogenic *F. oxysporum* or *P. fluorescens*, able to induced systemic resistance in the plant. The tools are now available to evaluate the diversity among natural populations of antagonistic microorganisms and study the selection pressure exerted by the plant. These studies are important to select efficient antagonists which are competent to colonize the roots of the host plants. This knowledge could also be useful to select disease management practices able to enhance the natural populations of biological control agents in soil.

Key words: biocontrol agents, soil-borne diseases, biological control, IPM , disease-suppressive soils.

Introduction

This paper will not review all the recent literature dealing with biological control of soilborne pests and pathogens since several books and many review papers have been recently published. On the contrary, this article will only focus on the approaches that have been followed to detect and select efficient biocontrol agents and to study their modes of action. Indeed, success of biological control requires a good knowledge of the modes of action of the antagonistic microorganisms. Most of the recent advances in that field of research have been made possible by the use of modern techniques of biochemistry and molecular biology that have permitted the demonstration of the role of antibiosis, competition for nutrients, parasitism or induced resistance in the mechanisms of biological control achieved by bacteria or fungi. These different modes of action are not exclusive from each other, on the contrary several of them can contribute together to control diseases. Therefore one of the most promising strategy to improve biological control consists in combining several modes of action either by associating several strains of biological control agents or by associating several modes of action in the same improved strain of biological control agent.

Disease - suppressive soils

A good approach to initiate research on biological control of diseases induced by soilborne plant pathogens is to look for field situations where disease severity remains low inspite of the presence of the pathogen, culture of susceptible cultivars and environmental conditions favourable to disease expression. Such healthy fields in an infested area usually indicate the existence of suppressive soils, i.e. of soils that limit the survival or activity of the pathogen. The hypothesis that such soils are suppressive to the disease is easy to test in greenhouse experiments. The pathogen is artificially produced and introduced at increasing concentrations into the soil and disease incidence on a susceptible host is compared to that produced by the same inoculum concentrations in a conducive control soil. All experimental conditions being comparable, differences in disease incidence have to be attributed to differences in the soil environment.

Soils suppressive to some of the most important

soilborne plant pathogens have been described; they control diseases induced by *Phytophthora cinnamomi*, *Pythium ultimum*, *Rhizoctonia solani*, *Thielaviopsis basicola*, *Gaeumannomyces graminis* and several formae speciales of *Fusarium oxysporum*. Several of the most efficient strains of biological control agents have been isolated from disease-suppressive soils, this is the case for strains of fluorescent *Pseudomonas* spp., nonpathogenic *Fusarium oxysporum*, nonpathogenic *Pythium* spp., *Trichoderma* spp. and *Gliocladium* spp.

However, it is always difficult to detect the microorganisms responsible for soil suppressiveness. Involvement of the soil microflora was achieved by demonstrating that the suppressiveness of the soil disappears upon destruction of organisms by biocidal treatments and can be restored by mixing small quantity of suppressive soil into a previously heat-treated soil (14). Then different approaches have been followed to determine among the microbial populations of the soil which was the population responsible for suppressiveness. Studying the fusarium-wilt suppressive soils from Châteaurenard, Rouxel *et al.* (17) established that suppressiveness disappeared after elimination of the populations of nonpathogenic *Fusarium* by heat-treatment at 55°C and reappeared after their reintroduction into the heat-treated soil. Scher and Baker (18) isolated strains of fluorescent *Pseudomonas* from mycelium mats of *F.oxysporum* buried in the suppressive soils from the Salinas Valley and demonstrated that introduction of some of these bacteria in a conducive soil made it suppressive to fusarium wilts. Defago *et al.* (5) chose to isolate fluorescent *Pseudomonas* spp. from the rhizosphere of plants growing in a suppressive soil and demonstrated their ability to control black root-rot of tobacco in conducive soils. In fact, there is not a single strategy to isolate efficient biological control agents, but isolation from suppressive soils or from plants growing in suppressive soils increases the probability of success.

Studies of the mechanisms responsible for disease suppression provided hypotheses about the modes of action of the antagonistic microorganisms involved in soil suppressiveness. Scher and Baker (19) established a correlation between the capacity of a strain of *Pseudomonas putida* to chelate iron and the demonstration that competition for iron was one of the mechanism responsible for soil suppressiveness to fusarium wilts. Indeed, the level of suppressiveness of the soil was either decreased or increased by addition of FeEDTA or EDDHA that respectively make iron more or less available for *F.oxysporum* growth. Introduction of either a bacterial strain or of its siderophore in soil reduced the rate of germination of *Fusarium* chlamydospores and the severity of fusarium wilt (6, 8). The antagonistic activity of pseudobactin was attributed to iron competition since the antagonism was suppressed when introduction of the siderophore was associated with iron (8). In the case of the suppressive soils from Châteaurenard, Alabouvette *et al.* (2) established that competition for carbon was one of the mechanisms responsible for suppression. Indeed, addition of glucose to the suppressive soil made it conducive. A correlation was established between competition for carbon and the activity of the biomass of the suppressive soil which was much more responsible to glucose amendment than the biomass of a conducive soil. This general competition for nutrients also controls the intensity of competition for carbon between pathogenic and nonpathogenic strains of *F.oxysporum*. It was established that the most effective strains of nonpathogenic *F.oxysporum* in biocontrol experiments are those which are the most efficient in glucose consumption (1). All these results provided good arguments in favour of the importance of competition for carbon and iron in the mechanisms of soil suppressiveness to fusarium wilts, but they did not prove that competition is the mode of action of the antagonistic microorganisms studied. Only the use of deficient mutants provided evidence of the modes of action of the biological control agents.

Modes of action of biocontrol agents

As stated above, recent use of molecular and biochemical techniques led to great progress in the understanding of the modes of action of antagonistic microorganisms.

- Antibiosis

Many strains of antagonistic bacteria have been selected for their ability to inhibit the growth of fungal pathogens *in vitro*. Therefore, one assumed that antibiosis was responsible for their efficacy in controlling disease. In the case of fluorescent *Pseudomonas* spp. which are producing siderophores and several other metabolites having inhibitory properties *in vitro* against fungi, it was very difficult to decide which was the predominant mode of action *in vivo*.

Thomashow and Weller (21) generated phenazin-deficient mutants of the strain 2-79 of *P. fluorescens* by Tn-5 mutagenesis. These deficient mutants failed to inhibit the growth of *G. graminis in vitro* and were significantly less suppressive than the parental strain to take-all of wheat. The mutants restored in their ability to produce phenazin, inhibited the growth of the fungus *in vitro* and were able to control the disease. These results permitted to attribute an important role to phenazin production in relation to the capacity of this strain 2-79 to control take-all in the fields. But it was still an indirect demonstration. Finally the presence of phenazin was detected in field soil and its presence in the rhizosphere of wheat was correlated with less disease on the roots.

Phenazin is not the only metabolite produced by this strain of *Pseudomonas fluorescens* and, if the phenazin deficient mutant was not as effective as the wild strain to control the disease it exerted some efficacy in comparison to the untreated control. Therefore, using the same strategy of generating mutants deficient for the production of different metabolites, Thomashow and Weller (22) were able to assess the relative importance of the phenazin antibiotic, the siderophore and the "antifungal factor" in control of take-all.

The same type of approach has been followed by Defago *et* al. (5) to demonstrate the role of cyanide production by *Pseudomonas fluorescens* strain CHAO in suppression of the disease caused by *Thielaviopsis basicola* and in the increased root hair formation in tobacco.

Since these first reports, this strategy based on transposon insertion mutagenesis, transfer of recombinant cosmids and gene replacement techniques has been widely used to demonstrate the role of antibiosis in biological control achieved by either bacteria or fungi.

- Induced resistance

Control of diseases achieved by antagonists may not only involved direct interactions between the biocontrol agent and the target pathogen but may be mediated through the plant. This phenomenon of induced resistance, also called systemic acquired resistance (SAR) or induced systemic resistance involves active resistance mechanisms of the host-plant activated by the biological control agent (9). It is well known that the preinoculation of a plant with a noncompatible forma specialis of *F. oxysporum* will delay symptoms after inoculation of the plant with its specific forma specialis (16). When the experimental design prevent any direct contact between the microorganisms (for example inoculation on each side of splitted root system) the short lasting protection observed must be attributed to induced resistance. But it is only recently that this phenomenon has been correlated with the accumulation of pathogenesis related (PR) proteins in the plants (20).

The fluorescent *Pseudomonas* spp. which can control several diseases through competition (see below) or antibiosis (see above) are also able to induce systemic resistance in the plant. The first evidence was provided by Van Peer *et al.* (23) with carnation grown on rockwool. The bacterial strain WCS417 and the pathogen were spatially separated by applying the pathogen in the stem and inoculating the roots with WCS417 one week earlier. The protection of the plant was correlated with a significant acceleration and increase of phytoalexin production in *Fusarium* inoculated stems. Moreover the use of heat-killed cells of WCS417 or of phenol-extracted lipopolysaccharides of WCS417 induced the same beneficial effect indicating that the LPS of the bacteria may be involved in the induced resistance. Recently the use of mutants of WCS417 deficient for LPS production allowed the demonstration of the role of these constituants of the bacterial wall in induced resistance (10). Since this first report on induced resistance by fluorescent *Pseudomonas* spp. studies have demonstrated the involvement of systemic acquired resistance in the control of diseases achieved by other strains of PGPR (9).

- Competition for nutrients

As stated above studies of soils suppressive to fusarium wilts indicated that competition for carbon and competition for iron were at least partly responsible for disease control. On the other hand, nonpathogenic strains of *F.oxysporum* and strains of fluorescent *Pseudomonas* spp. were able to induce suppressiveness in conducive soils. Whether these microorganisms were responsible of the observed phenomenon of competition has only recently been demonstrated. Lemanceau and Alabouvette (11) established that some strains of fluorescent *Pseudomonas* spp., thought not effective on their own, improved significantly the control achieved by Fo47 a nonpathogenic strain of *F. oxysporum*, which has been demonstrated to suppress fusarium wilt significantly (3). Then it was shown that the combination of Fo47 with WCS358, a strain of *Pseudomonas putida*, significantly reduced the percentage of diseased carnations, even when these strains were not efficient on their own. Since the mutant of WCS358 deficient for the production of siderophore had no effect in combination with Fo47, it has been concluded that the beneficial effect is related to siderophore production (12). It was also demonstrated that the intensity of the intraspecific competition for carbon between pathogenic and nonpathogenic *F. oxysporum* depends on iron availability controlled by the activity of siderophore producing *Pseudomonas* spp. *In vitro*, the pathogenic *F. o.* f.sp. *dianthi* was much more sensitive to competition for carbon than the nonpathogenic strain Fo47 and its growth yield (defined as the germ-tube length per unit of glucose consumed) was reduced when the availability of iron was decreased by addition of the pseudobactin produced by the strain WCS358 of *Pseudomonas putida* (13). These results provided a good explanation for the synergistic effect of the coinoculation of nonpathogenic *F.oxysporum* with fluorescent *Pseudomonas* spp. to control fusarium wilts of several crops and demonstrated that competition for carbon and competition for iron are not independent from each other.

The importance of competition for nutrients in the mechanisms of biological control is always difficult to demonstrate experimentally but there is indirect evidence of the role of competition in the modes of action of

several biological control agents.

Complementarily of modes of action of biocontrol agents

Competition for nutrients, antibiosis, induced resistance are not the only mechanisms by which biocontrol agents can achieve control of diseases due to soilborne plant pathogens.

Mycoparasitism is another important mode of action explaining the efficiency of *Sporidesmium sclerotivorum* in controlling diseases induced by sclerotia forming plant pathogens and of *Verticillium biguttatum* in controlling *Rhizoctonia solani* in potato. These two fungi behave as obligate parasites of sclerotia, that will be destroyed by colonization of the mycoparasite. The following reduction of inoculum density in soil will result in a decreased incidence of the disease.

Other fungi, such as strains of *Trichoderma* spp. may be active through parasitism of the plant pathogen, but they are also producing different types of metabolites antagonistic to other microorganisms, they can even induce resistance in the host plant. *Trichoderma* spp. as fluorescent *Pseudomonas* spp. and nonpathogenic *Fusarium* spp. all present several modes of action which contribute to their efficacy as biocontrol agents. Depending on the target pathogen and on the host plant several modes of action are cooperating to achieve biological control. Studies of soil suppressive to fusarium wilts illustrated the fact that the more complex are the mechanisms of suppression, the more diverse are the antagonistic populations, the more consistent and durable is the control of the disease. At the present time, many teams tend to associate different modes of action to achieve biological control. The easiest way to combine several modes of action is to use an association of several antagonists each having different modes of action. Following this approach, Alabouvette *et al.* (4) are utilizing the association of *F. oxysporum* Fo47 with *P. fluorescens* C7 to control fusarium wilts of vegetables and flowers grown in soilless cultures in greenhouses. However this approach is facing problems difficult to solve. As the fungus and the bacteria are having different requirements for growth and survival, it will probably not be possible to formulate both biocontrol agents in a single product easy to handle and apply.

A more elegant approach than the previous one, consists of associating several modes of action in the same strain of a biological control agent using techniques of molecular biology. Such approach was initiated by Voisard *et al.* (1993) who reported that a recombinant of *P.fluorescens* P3 with the HCN genes from CHAO showed an improved biocontrol activity against black root rot of tobacco. Weller and Thomashow (25) also transfered phloroglucinol production from the strain 92-97 into the phenazin producer strain 2-79 and observed an increased inhibition of several plant pathogenic fungi *in vitro*. It is also possible to induce an increased production of biocontrol metabolite by introducing extra copies of biosynthetic or active genes. This transfer of genes important for biological control is easier to realize with bacteria than with fungi. However, Harman *et al.* (7) described techniques useful to identify fungal genes of *Trichoderma* and *Gliocladium* responsible for lytic activities and methods for genetic manipulation of these fungi. One may assume that fungal biocontrol agents with several modes of action will be available in the near future.

Whether these biological control agents will be registered and accepted by the public is another question that will not be debatted here.

Conclusion

Though progress has been made in the understanding of the modes of action of antagonistic microorganisms, only few biocontrol agents are available on the market to control soilborne pests and pathogens. Selecting a strain efficient under experimental conditions and identifying its modes of action only represent the first step toward biological control in the field. Mass production, formulation and application of the biocontrol agents also require important studies that have to be conducted in cooperation with industry and farmers. Specific problems linked to development of biocontrol products have been recently reviewed (15, 26) and one must say that they have been frequently underestimated by scientists more interested by the mode of action of the antagonists than by their practical application.

The choice of the culture medium for mass production and the type of formulation both condition the efficacy of the biocontrol agent. The physiological state of the inoculum seems to play an important role in relation to survival and efficiency of the biocontrol agent. Many reports indicated that survival and efficiency are not directly correlated, old propagules able to give rise to a colony on agar medium might be no more effective in controlling the disease. More research is needed in that field. It is also necessary to consider other cultural and control practices to integrate the biological control strategy in the cropping system. Indeed, most of the biocontrol agents are target specific, i.e. they control a single disease. Therefore they must be compatible with the control measures including pesticides that are needed to control other pests or pathogens affecting the same crop. Moreover the efficacy of the biocontrol may be dependent on environmental factors that have to be considered. For example, it has been demonstrated that efficacy of fluorescent *Pseudomonas* spp. acting through competition for iron depends on iron availability and

therefore will be increased if iron is provided to the plant as FeEDDHA. Biological control will probably always require more care of the cultural conditions than chemical control.

Finally, a biocontrol agent to be registered must satisfy several criteria of nontoxicity to humans and animals and of being safe to the environment. If the risks linked to the introduction of biological control agents in soil or with plant materials have to be considered they should not be overestimated.

Recent advances made in biological control of soilborne pests and pathogens let us expect a greater use of biological control in the near future, but it must be emphasized that biological control will not solve all the problems and that it has to be used in association with other control methods such as cultural practices, genetic plant resistance and chemical control at reduced dosage.

الملخص

آلابوفت، س. 1995. التطورات الحديثة في المكافحة الأحيائية للآفات والأمراض المنقولة مع التربة. مجلة وقاية النبات العربية. 13(1): 46-41

تم، بشكل عام، اتباع طريقتين للمكافحة الأحيائية للآفات والأمراض المنقولة مع التربة: أ) تسريع الإمكانية الطبيعية للتثبيط الموجودة في كل الأتربة و ب) إدخال سلالات محسنة من الكائنات الحية الدقيقة المضادة الموجودة في الطبيعية. وتحتاج كلتا الطريقتين إلى معرفة جيدة بحياتية الكائنات المستهدفة وبيئياتها وبحياتية وبيئية عوامل المكافحة الأحيائية. ويجب أن تكون عشائر الكائنات المضادة أو المدخلة متخصصة على الكائن المستهدف، وأن تكون موجودة ونشطة في المكان والزمان الذي يكون فيهما الممرض حساساً لنشاطها التضادي. وقد حدثت تطورات كبيرة في الطرائق البيوكيميائية والجزيئية لفهم طرائق عمل عديد من عوامل المكافحة كأنواع *Trichoderma* وأنواع *Pseudomonas* المومضة، والأنواع غير الممرضة من فطر *Fusarium oxysporum*. وتفيد المعلومات عن طرائق عمل هذه الكائنات في أ) تحسين طرائق انتخاب عوامل المكافحة الأحيائية الواعدة، ب) اختبار السلالات التي تمتلك طرائق عمل مختلفة لاستخدامها مع بعضها، جـ) اختيار فضلى الشروط لإنتاج عوامل المكافحة الأحيائية، وتحضيرها واستخدامها. وتشير على سبيل المثال ان وجود سلالة غير ممرضة من *F. oxysporum* التي تنافس الممرض على مصدر الكربون مع سلالة *Pseudomonas* المومضة التي تنافس الممرض على الحديد أدى الى تحسن في مكافحة مرض الذبول الفيوزاريومي على البندورة/ الطماطم والقرنفل. ولتحسين الأثر الطويل المدى لهذه المكافحة، قد يكون من المفيد استعمال سلالة ثالثة من كلا العاملين السابقين بمقدورها بدء مقاومة جهازية في النبات. وتتوافر حالياً الوسائل لتقويم التنوّع في مجتمعات الكائنات الحية الدقيقة المضادة ودراسة ضغط الإنتخاب الذي يمارسه النبات. ولهذه الدراسات أهميتها في انتخاب الكائنات المضادة القادرة على استعمار جذور العائل، كما أنها تفيد في انتخاب ممارسات إدارة المرض القادر على تحفيز المجتمعات الطبيعية لعوامل المكافحة الأحيائية في التربة.

كلمات مفتاحية: عوامل مكافحة أحيائية، أمراض منقولة مع التربة، مكافحة أحيائية، أتربة مثبطة للممرضات.

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