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EFFECT OF SOIL PHYSICAL FACTORS ON BIOLOGICAL CONTROL AGENTS OF SOIL INSECT PESTS

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ABSTRACT

An appreciation for the complexity of the soil environment is important when developing strategies for biological control of soilborne insect pests. Basic principles of soil physics and the effects of soil physical factors on entomopathogenic nematodes and fungi are reviewed, and areas for future research are suggested.

RESUMEN

Una consideración de la complejidad del ambiente del suelo es importante en el desarrollo de estrategias para la aplicación o mejoramiento del control biológico de plagas del suelo. Se revisan algunos principios básicos de la física del suelo y el efecto que los factores físicos tienen sobre los agentes de control biológico, y se sugieren futuras áreas de investigación.

Many economically important insects spend some portion of their life in the soil, and often these stages are destructive to crops (Villani & Wright 1990). Interest in biological control has increased because of concerns about the economic, environmental, and health costs of chemical crop protection practices (Hoy & Herzog 1985). Insect pathogens in particular show promise as biological control agents in soil (Fuxa 1987, Klein 1988). Soil can provide favorable physical conditions for survival of entomopathogens. For example, in comparison to the aerial environment, pathogens in soil are not subject to destruction by solar radiation, and humidity is relatively high and stable.

An appreciation for the complexity of the soil environment is important when developing strategies for biological control of soil insects. Many attempts at biological control have been made without adequate understanding of the ecology of the control and target organisms, resulting in inconsistent biological control (Ehler 1990). Soil is a dynamic system that responds to environmental changes and energy supply (Moore et al. 1988). In addition to physical factors (e.g., soil texture and structure, soil water status, gases, temperature, pH), numerous biotic factors (e.g., host population, host-plant of target insect, predators and antagonists of the biological control agent, alternate hosts) influence both infection and spread of disease in insect populations (Lingg & Donaldson 1981, Boethel & Eikenbary 1986, Fuxa 1987, Groden & Lockwood 1991). Human actions also influence biological control through agricultural production practices such as tillage, irrigation, pesticide and fertilizer application, and crop plant variety selection.

Villani & Wright (1990) recently provided an excellent review of the effects of soil physical factors on soil-inhabiting insects. The purpose of this paper is to review some basic principles of soil physics, and illustrate the effects of soil physical factors on biological control agents. Examples will be from two groups that are currently receiving much research attention because of their promise for commercial development as control agents for soil-inhabiting insects—entomopathogenic fungi in the genera *Beauveria* and *Metarhizium*, and nematodes in the genera *Steinernema* and *Heterorhabditis* (McCoy 1990, Kaya 1990). While it is not always possible to generalize on the effects of soil physical factors on biological control agents, these two groups are representative of two different types of infection strategies. Steinernematid and heterorhabditid nematodes possess a non-feeding, motile, infective stage, and host-finding in soil by this stage is a critical component of parasitism of insects (Schmidt & All 1979). In contrast, although some growth of *Beauveria* and *Metarhizium* occurs in soil (Gottwald & Tedders 1984), most infections are dependent on a motile host contacting the non-motile, infectious conidiospores in soil (Ferron 1981).

Soil Physical Factors

Soil consists of three dynamic phases—the soil matrix, soil solution, and soil atmosphere (Hillel 1982). These phases vary in time and space and are affected by variables such as weather, vegetation, and soil management. The effects of different soil physical factors are interrelated and often difficult to separate. For example, soil texture and structure affect moisture holding characteristics; temperature affects moisture; and moisture and temperature affect soil atmosphere and chemistry.

Soil Matrix

The soil solid phase is composed of discrete mineral particles of various sizes and amorphous organic compounds coating the particles (Brady 1974). Soil texture refers to the size range of particles in soil. The particles are traditionally divided into size range categories known as textural fractions: sand, silt, and clay. There are several classification schemes, but sand particles generally range in diameter from 50 um to 2000 um, silt from 2 um to 50 um, and clay less than 2 um. Textural class is determined on the basis of the mass ratios of the three fractions of soil.

Most research on matrix effects on biological control has been concerned with soil texture. Different size organisms have different amounts of space available to them due to soil texture. Smaller particle size and finer soil texture results in increased tortuosity that can impede the movement of soil organisms and effectively increase the distance travelled from one point to another. Based on texture alone, sandy soils generally have larger pores, less tortuosity and better aeration than clay soils.

Soil structure refers to the arrangement of soil particles into aggregates of varying size, geometry, and porosity (Hillel 1982). Structure is strongly affected by climate, biological activity, density and continuity of surface cover, and soil management practices. Structured pore space is largely determined by size and arrangement of aggregates and affects the movement of water, air, and organisms in soil. Soils that are coarse textured are less likely to have a well-defined structure and therefore fewer structured pore spaces than a soil high in clay content. Structured pore space decreases with depth and compaction.

Ecological relationships among soil organisms are influenced by soil structure (Elliot & Coleman 1988). Macropores, usually created by earthworms and roots, serve as the principal avenues for infiltration and drainage of water and for aeration, and provide a relatively continuous path for movement of microarthropods. The next smaller size of structured pore space, the intermacroaggregate (macroaggregates are ±2 mm diameter), is large enough to be inhabited by nematodes. Still smaller, the intermicroaggregates (microaggregates are ±0.1 mm diameter) are large enough to accommodate small nematodes, protozoa, and fungi. The smallest class of structural pore, the intramicroaggregate, is <1 um in diameter and is large enough for bacteria.

Soil texture effects on nematode motility, infectivity and survival have been studied. Migration of *Heterorhabditis* sp. and *Steinernema glaseri* and infection of larval sheep blowfly, *Lucilia cuprina*, were lower in clay soils than in sandy soils. Parasitism by the larger nematode, *S. glaseri* (45 um diam.), was lower in soils of high clay content (Molyneux & Bedding 1984). In organic, clay and fine sandy loam soils, *S. carpocapsae* (25 um diam.) moved least in organic soil and most in fine sandy loam, and *H. bacteriophora* (25 um diam.) moved least in clay soil and most in fine sandy loam soil (Barbercheck & Kaya 1991a). Survival and infectivity of *S. carpocapsae* and *S. glaseri* in four soils decreased as the proportion of clay increased, and Kung et al. (1990a) attributed this to larger particle sizes and better aeration in sandy soils.

Contact between soilborne entomopathogenic fungi and the target soil insect is determined largely by soil factors affecting passive percolation into the soil profile (texture, structure, and organic matter), and the activity and location of the target insect relative to the control agent. Differences in vertical distribution of *Nomuraea rileyi* conidia occurred with respect to soil texture (Ignoffo et al. 1977). Conidia adsorbed onto clay particles in a silt loam soil and conidia were restricted mostly to the upper 2 cm, whereas conidia readily penetrated river sand. In contrast, adsorption to clay particles was not observed with commercially formulated *B. bassiana* (Storey & Gardner 1987). Retention of conidia in soil columns of sifted soils was positively correlated with sand composition and negatively with clay composition. However, vertical penetration of *B. bassiana* conidia was similar in undisturbed soil profiles of four soil types covering a range of clay:sand ratios, and >94% of the conidia were recovered in the upper 5 cm of each profile (Storey & Gardner 1988). In a field trial, distribution of *B. bassiana* conidia in the soil profile was similar in conventional tillage and no tillage treatments in sandy clay loam soil and most conidia remained in the top 5 cm of the soil (Storey et al. 1989). Retention of conidia in the upper soil profile was caused by mechanical filtration within the soil structure.

There is evidence that solid components, especially some types of clay minerals, affect microbial activity. This effect may be indirect and due to the ability of clay to protect microorganisms against inhibitory effects of osmotic potential. Clays can protect propagules of *B. bassiana* from biodegradation by antagonists (Fargues et al. 1983, Studdert et al. 1990).

Soil Solution

The variable amount and energy state of water in the soil are important factors influencing organisms, soil aeration, and gas exchange. Liquid water in soil is described in terms of soil wetness (per mass or per volume fraction of water in soil) or the force per unit mass with which water is held to soil (potential, tension, or suction) (Hillel 1982). Although it is common for entomologists to measure soil moisture in terms of

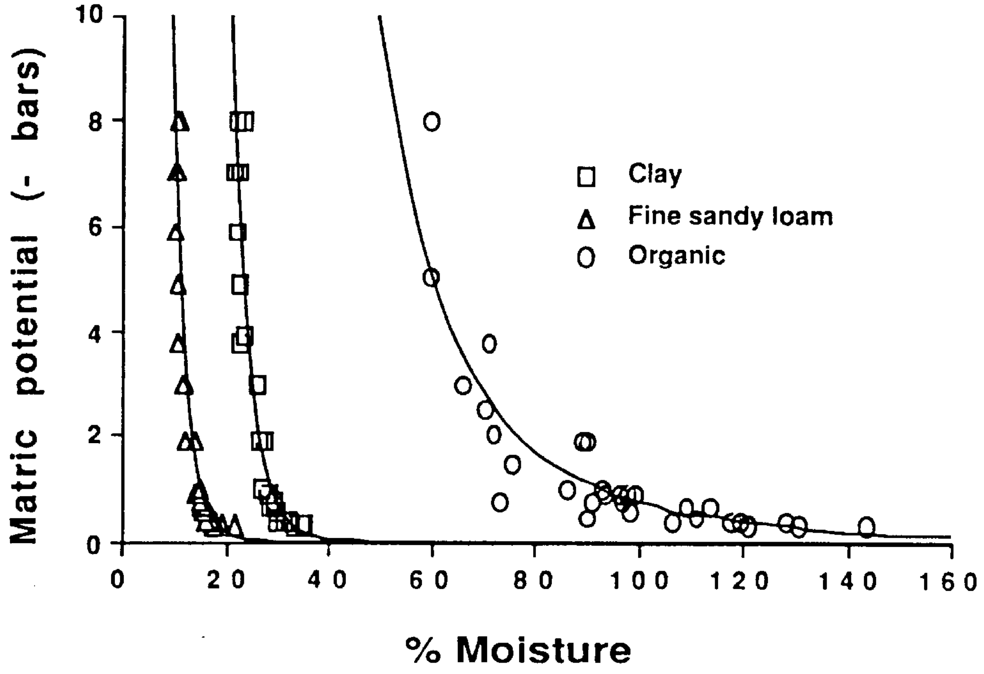

Fig. 1. Relationship between soil matric potential and percent soil moisture (v/dry wt.) in organic (50% sand, 35% silt, 15% clay, 40% OM), clay (22% sand, 43% silt, 35% clay, 2% OM), and fine sandy loam (51% sand, 33% silt, 16% clay, 0.9% OM) soils.

percentage moisture, the use of water potential has more ecological significance and allows comparison of results across many soil types. The same percentage moisture in soils of diverse texture may represent extreme differences in potential (Fig. 1). Potentials are usually reported as negative numbers and decreasing potential is correlated with decreasing wetness and thickness of water film around the soil particles. At saturation, water potential is zero. As drying occurs, large (>50 um) pores drain first at field capacity (approx. -0.1 bar). A gradual decrease in potential results in emptying of progressively smaller pores. Storage pores (50-0.5 um) hold water against drainage between field capacity and permanent wilting point (approx. -15 bars). At very negative water potentials very narrow pores (<0.5 um) retain water that is unavailable to plants(<-15 bars) (Table 1).

Water potential is the primary factor determining the availability of soil water to plants and animals. In general, nematodes, protozoa, and bacteria require a water film for activity, whereas fungi and microarthropods do not. Consequently, the pore size distribution and distribution of water in the pore space can differentially affect the activity of various organisms. As water potential decreases, and progressively smaller pores become drained, the water-filled pathway for activity of motile stages is diminished. Soil texture and structure are also important because they determine the frequencies of the different pore sizes. For example, most pores in an unstructured clay are 20 um in diameter or smaller. Consequently, even when the soil is saturated, organisms dependent for motility on pores larger than 20 um will be immobile in clay, because pores of adequate size are infrequent in soils of fine texture (Wood 1989).

Nematodes require water films of sufficient thickness and continuity to allow movement. However, as moisture increases, air-filled pore space decreases, and aerobic respiration is inhibited. In wet or saturated soils, nematode movement can be restricted due to lack of surface tension forces necessary for movement (Wallace 1971). When the

TABLE 1. RELATIONSHIP OF WATER POTENTIAL TO RELATIVE HUMIDITY AND DRAINAGE OF PORES IN SOIL.[a]

Water potential (–bars)[b]	Relative humidity (%)	Diameter of largest water-filled pores (um)
0.0	100.0	inf.
0.001	99.9	2,908.000
0.01	99.9	291.000
0.1	99.9	29.100
1.0	99.9	2.910
10.0	99.3	0.291
20.0	98.5	0.145
100.0	92.9	0.029

[a] After Brady 1974.

[b] Field capacity is approximately –0.3 bars, permanent wilting point is approximately –15 bars, –1 bar = –100 KPa.

water films become about 1 um thick surface tension forces hold the nematodes too tightly against the soil particle to allow movement. Movement in dry soil may also be restricted because nematodes become quiescent or anhydrobiotic (Womersley 1990). LC_{50}s for *S. carpocapsae* in *Spodoptera exigua* were lower in moist (–1 bar) organic, clay, and fine sandy loam soils than in the same drier (–3 and –8 bars) soils. LC_{50}s for *H. bacteriophora,* not as clearly affected by soil moisture, were lowest at –1 bar in clay, at –1 and –3 bars in fine sandy loam, but there was no significant difference between moisture levels in organic soil (Barbercheck & Kaya 1991b). Parasitism of *L. cuprina* by *Heterorhabditis* sp. occurred at low moisture potentials in loamy sand, and in nearly saturated soils in sand (Molyneux & Bedding 1984).

Free water can adversely affect fungal propagules. Survival of conidia of *B. bassiana* is greater in soils with low organic matter content and decreases as soil moisture content increases (Lingg & Donaldson 1981, Studdert et al. 1990). *B. bassiana* conidia half-lives were longest in non-sterile soil at –15 bars, and decreased as soil became moister or drier (Studdert et al. 1990).

pH Of The Soil Solution

Soil is a heterogeneous system and the pH of microsites may vary considerably from the average pH of bulk soil. Alkalinity occurs in soils with high base saturation or in the presence of salts and is characteristic of most arid and semiarid regions. In saline soils microorganisms face problems of high concentrations of ions above their normal intracellular concentrations, which may lead to disruption of cell function. Acid soils occur around the world, especially in the humid tropics. Acid soils have a low percentage base saturation and a greater number of H^+ ions on clay and organic matter. Clays with high amounts of exchangeable H^+ are not stable, dissolve, and release aluminum, magnesium and silica (Brady 1974). Little is known about the mechanisms of aluminum toxicity to insect pathogens in soil even though this may be a major factor limiting microbial growth and activity in acid soils (Wood 1989).

The pH of the soil solution may affect biological control. Acidic soil with pH levels below 4.0 limited infection of *Cephalia abietis* by *Steinernema kraussei* (Fischer & Führer 1990). In sandy loam soils set at pH 4, 6, 8, and 10, survival and retention of infectivity of *S. carpocapsae* and *S. glaseri* were greatest at pH8. Survival of both species dropped sharply after 1 week at pH10 (Kung et al. 1990b). Half-lives of conidia of *B. bassiana* were similar at pH5, 6, and 7.6 (Lingg & Donaldson 1981). Fungistasis levels against germination of *B. bassiana* conidia increased exponentially with increases in soil pH from 5.1 to 7 (Groden & Lockwood 1991).

Soil Atmosphere

Average atmospheric air contains 79% N_2, 21% O_2, and 0.03% CO_2, whereas the average arable topsoil atmosphere contains 79% N_2, 20.3% O_2, and 0.15 to 0.65 % CO_2. Under extreme conditions oxygen in topsoil has been recorded as low as 1%, and soil CO_2 has been recorded as high as 10%. Oxygen percentage in soil decreases with depth and the rate of decrease is more rapid in clayey or silty soils than in sandy soils (Brady 1974).

Soil aeration is dependent on the fraction of air-filled pores and macroscopic pores drain quickly and are nearly always air filled. Therefore, lack of oxygen is unlikely to limit biological activity at low water potentials. However, at higher water potentials many of the pores are filled with water, and oxygen may become limiting. Organisms in fine-textured soil aggregates may be adversely affected by localized anaerobic conditions. In a study of survival and infectivity of *S. carpocapsae* and *S. glaseri* in sandy loam soil at oxygen concentrations between 1 and 20%, survival of both species decreased significantly after 8 weeks as the oxygen concentration decreased from 20 to 1%. No nematode pathogenicity was recorded at oxygen concentrations of 1, 5, or 10% after 2 weeks or at 20% after 16 weeks (Kung et al. 1990b).

Under normal agricultural field conditions, where moisture levels are kept high enough to support crop growth, the soil atmosphere is nearly always vapor saturated (Table 1). This condition is physically conducive for biological control of soil insects by organisms that require high relative humidities, such as entomopathogenic fungi and nematodes. Even at permanent wilting point, relative humidity in the soil is usually sufficient for fungal germination and growth (Griffen 1963). Relative humidities above 92.5 and 85% are needed for spore germination, mycelial growth, and sporulation of *Beauveria* and *Metarhizium*, respectively (Walstad et al. 1970). A high RH is conducive to germination, but not necessarily to spore longevity (Walstad et al. 1970). A decrease in conidial survival with increased moisture may be a result of reduced oxygen, although oxygen and carbon dioxide concentration may have little effect on conidia as long as they are dormant (Lingg & Donaldson 1981). Steinernematid and heterorhabditid nematodes can survive $RH<97\%$ in an inactive state provided that desiccation occurs slowly (Womersley 1990).

Soil Temperature

Soil temperature governs the rates and directions of soil physical processes and chemical reactions, and influences biological processes. Temperature, and its interaction with moisture, is one of the most important physical factors influencing the infection of soil-inhabiting insects by entomopathogenic fungi (Hall & Papierok 1982). Different pathogen species and strains have different thermal limits for survival, germination, and infection, and temperature thresholds for survival and growth probably depend on the geographical origin of the organism. Peak in vitro germination of *B. bassiana* and *M. anisopliae* occurs at 25°-30°C, with a germination range of 15° to 35°C. Sporulation occurs between 10° and 35°C, and the thermal death point for both fungi is approximately 50°C. Conidia of both species survived >1 year at 8°C, but at 21°C, *B. bassiana* survived for 0.5 months and *M. anisopliae* for 2.5 months (Walstad et al. 1970). Half-life values of *B. bassiana* conidia in non-sterile fine sandy loam and peat soils at –10 bars were greatest at 10°C and decreased with increasing temperatures (Studdert et al. 1990). *B. bassiana*-induced mortality of pupal beet armyworm, *Spodoptera exigua*, in non-sterile fine sandy loam and peat soils at –0.3 bars increased as temperature increased from 8° to 24°C (Studdert & Kaya 1990). The *in vivo* incubation period of *B. bassiana* (exposure rate 2.3 × 10^4 CFU/cm^2) in the European corn borer, *Ostrinia nubilalis*, varied in response to incubation temperature from 20 days at 10°C to 8 days at 25°C in 5th instar larvae (Carruthers et al. 1985).

There is considerable inter- and intraspecific variability in temperature tolerances among entomopathogenic nematodes. Among 16 species and strains of the genera *Heterorhabditis* and *Steinernema* the lowest temperatures of activity among heterorhabditids ranged from 10° to 16°C, and among steinernematids from 3° to 14°C. Steinernematids were more active at lower temperatures and were active over a greater temperature range than heterorhabditids, but the temperature range of infectivity differed between nematodes of the same genus and strains of the same species (Molyneux 1986). Persistence and infectivity of *S. carpocapsae* against the lesser mealworm, *Aliphitobius diaperinus*, in sandy loam soil decreased with increasing temperatures from 20° to 32°C (Geden & Axtell 1988).

Soil Physical Factors and Relative Competitive Advantage

As noted previously, soilborne organisms are affected by soil physical factors. Physical conditions vary in time and space, and affect some organisms more severely than others, depending on their physical optima and limits for survival and activity. How the organism reacts to particular physical conditions affects the "relative competitive advantage" of the organism, i.e., the advantage of one organism over another as determined by their respective survival and growth rates under a particular set of physical conditions (Baker & Cook 1974). In competition studies between *B. bassiana* and *S. carpocapsae* or *H. bacteriophora*, *B. bassiana* was more likely to develop to the exclusion of nematodes in insects exposed first to the fungus and subsequently to nematodes at 15°C, while nematodes were more likely to develop at 22° and 30°C (Barbercheck & Kaya 1990). In dual exposure treatments of beet armyworm to *B. bassiana* and *S. carpocapsae* or *H. bacteriophora*, nematodes were more severely affected by decreasing water potential than was *B. bassiana* (Barbercheck & Kaya 1991b).

CONCLUSIONS

It is likely that the potential of successful biological control is greater in some soil environments than others. An understanding of the effects of environmental factors on biological control in soil is needed so that the most appropriate species to give optimal insect control can be used. Recently, Ehler (1990) discussed the need for a theoretical and predictive basis for biological control in the soil. Currently, we cannot generalize on field conditions under which biological control in soil will be successful.

Research on general soil ecology, and ecology of soilborne biological control agents is critical to determine what properties confer superior competitive ability against other soil organisms. Biotic interactions, e.g., competition and antagonism, and their mediation by physical conditions, are probably critical to biological control in the soil. Although research on antagonists and predators of biological control agents in the soil is increasing, this area is still relatively unstudied. Consequently, it is difficult to predict the likely fate of an introduced organism in soil. Strains of biological control agents adapted to the climate and soils of local conditions should be identified and studied. It may be possible to identify "pest-suppressive" and "biological control agent-suppressive" soils that can be studied to improve our ability to successfully use biological control in the soil.

Laboratory, greenhouse, and field experiments in which physical and biotic factors are manipulated should be conducted to identify conditions which favor biological control. Although it is useful to simplify the soil system in the laboratory or greenhouse, extrapolation from simplified microcosms to the field is difficult. Microenvironment in the field can be altered by practices such as irrigation, planting density, and variety selection and numerous other factors. To understand the influence of physical factors on biological control in soil it is essential that, whenever possible, physical data be collected. These data should be collected in a way that will allow comparison between experiments, for example, the use of water potential rather than percentage water to measure soil moisture. Both successful and unsuccessful field trials should be followed up to understand the mechanisms underlying the success or failure of biological control.

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BIOLOGICAL CONTROL OF WEEVILS AND WHITEGRUBS ON BANANAS AND SUGARCANE IN THE CARIBBEAN

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ABSTRACT

This review examines the major weevil and whitegrub pests on bananas and sugarcane of present economic concern in the Caribbean, as well as the various categories of biocontrol agents. It discusses their roles in reducing populations of these pest. Several successful biocontrol agents are presented together with recently obtained information that may affect practical biocontrol. Some directions of future research in this field are predicted. Emphasis will be made on *Cosmopolites sordidus* on banana and *Diaprepes abbreviatus* on sugarcane, targets of the main biological control attempts.

RESUMEN

Se revisan las mayores plagas coleopteras del suelo en banano y cana de azucar. Estas plagas representan un problema de tipo economico, y se consideran aqui varias categorias de control biologico. Se discute su importancia en la reduccion de las poblaciones de estas plagas. Se presenta informacion reciente la cual puede afectar el uso practico de varios agentes de control biologico. Se dan sugerencias y predicciones sobre la futura investigacion en esta area. El mayor enfasis de la investigacion en control biologico debe ser en las plagas mas importantes, *Cosmopolites sordidus* en banano y *Diaprepes abbreviatus* en caña de azucar.
