

Review

Compost: A study of the development process and end-product potential for suppression of turfgrass disease

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Summary

The relationships among the chemical, physical and biological aspects of compost and their role in suppression of turfgrass pathogens are reviewed. The composting process, mediated by microbial activity, is affected by physical and chemical characteristics which include temperature, aeration, moisture content, C:N ratio and pH. In the absence of parameter restrictions, the microbial community follows a predictable successional pattern resulting in the re-colonization of compost with metabolically active mesophilic populations that can be suppressive towards plant pathogens. Although mechanisms of suppression are not fully understood, those postulated include physiochemical and biological characteristics. The physiochemical characteristics of composts can alter suppressive properties through direct effects on pathogens and antagonistic microorganisms, or indirect effects on host systems through the supply of nutrients, improvement of soil structure, porosity and water retention capabilities, along with other factors. Biological characteristics centre on microbial community involvement in suppressive mechanisms, which can include one or a combination of competition for nutrients, antibiosis, lytic and other extracellular enzyme production, parasitism, predation and host-mediated induction of resistance. As a result of the potential benefits of compost, there is considerable interest in determining the capacity for composts to suppress turfgrass pathogens. Although the exact mechanisms of suppression are largely unknown, there appear to be several factors that play an integrated role. The use of composts that successfully suppress turfgrass diseases will permit a reduction in the use of chemical controls, and slow the development of fungicide resistance.

Introduction

The belief that composting is a means of decomposing organic matter to create a soil-conditioning product is too restrictive. Composting has been defined as intense microbial activity leading to decomposition of most biodegradable materials, usually mixtures of organic materials, which results in organic residue stability (Adani et al. 1997; Weltzien 1991). This process is considered to be the most efficient treatment in producing an environmentally safe and agronomically advantageous soil organic amendment at acceptable operational costs (Senesi & Brunetti 1996). Composting involves the complete or partial degradation of a variety of chemical compounds by a consortium of microorganisms, the composition of which changes as composting progresses (Whitney & Lynch 1996). The microbial community in compost converts degradable organic matter into more stable, humified forms and inorganic products (CO₂, H₂O, ammonia, nitrate, methane), and releases heat as a metabolic waste product (Ciavatta

et al. 1993). Characteristics of the microbial populations and their rate of change depends on the substrate and physical conditions under which composting takes place (Whitney & Lynch 1996).

Among the various processes used to manage organic wastes (e.g. land-fill, incineration), only the biological process of composting results in stabilization of such wastes, allowing a more complete recovery of resources and alternative use endpoints (Beffa et al. 1996b; Finstein et al. 1983; Zucconi et al. 1981). Benefits of composting range from a decrease in mass and volume of organic wastes, recycling of nutrients, maintaining or restoring organic matter and other important soil physical characteristics, reduction in land-filling problems, and biodegradation of toxic compounds and other organic contaminants (Adani et al. 1995; Gomez 1998; Insam et al. 1996; Sesay et al. 1997). The result is the creation of a valuable, stable, end product through the increase of nutrient retention and availability, cation exchange capacity, and humic components that serve as a source of organic matter (Sesay et al. 1997). Compost

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can be considered a soil conditioner that contributes to soil fertility, structure, porosity, organic matter, water holding capacity, cation exchange capacity, and disease suppression, provided it is properly prepared (Itavaara *et al.* 1997; Sesay *et al.* 1997; Zucconi *et al.* 1981).

The area of disease suppression is a more recently established alternative use of compost. Interest in biological control of pathogens has increased due to concern over pesticide use, occurrence of pesticide resistance in some pathogens, and lack of chemical controls or resistant plant varieties (Whipps 1997a). Fungicides have been successful in turfgrass disease management but, because of reliance on preventative management programs, excessive and unnecessary applications have resulted in selection of fungicide-resistant populations (Craft & Nelson 1992). The increasing use of fungicides has invoked concerns over environmental consequences of high application rates, toxic residues, health hazards of handling and application, elimination of non-target organisms from the agroecosystem, and concentration of chemicals up the food chain (Weltzien 1991; Nelson 1992). Other problems with high fungicide use include fungicide-enhanced disease resurgence, which refers to the return of diseases with increased severity after treatment (Couch 1995). Fungicide use also has effects on microbial populations in soil such as on mycorrhizal growth and development (Couch 1995). Many fungicides are detrimental to mycorrhizal associations, including benomyl, chlorothalonil, quintozene, triadimefon, anailazine, mareb, chloroneb, and iprodione (Couch 1995). The high frequency of chemical use, associated costs, and health risks to humans and the surrounding environment has led to an increase in the challenge for effective management of turfgrass diseases (Nelson 1992; Fokkema 1993).

Disease suppression has created a new interest for many industries that are dependent on commercial pesticide use, and are in need of effective alternatives. The turfgrass industry represents a sector where the use of composted material has potential to be beneficial, both ecologically and economically. The development of a standardized method of composting through the utilization of consistent combinations of feedstocks and cultural practices and monitoring of microbial community dynamics may allow for development of a product that is both stable and consistently suppressive to disease.

Composting Process

The composting process undergoes many fluctuations in chemical, physical and biological parameters. Successful composting is the result of a continual supply of basic needs to the microbial community: moisture, oxygen, temperature control and adequate mixing. In the absence of parameter restrictions, the microbial community follows a predictable successional pattern: mesophilic zymogenous, thermophilic, and finally mesophilic autochthonous organisms (Herrmann & Shann 1997). The two most important aspects of a compost process are its chemical makeup and the existing population of microorganisms. The composting process at the microbial level involves several interrelated factors: temperature, aeration, moisture, C:N ratio, pH, metabolic heat generation, available nutrients, and physical state of the material (Beffa et al. 1996b; Sartaj et al. 1995). The main biological components are the microbial populations which are important to decomposition efficiency. Because the breakdown of organic materials is dependent on thermophilic conditions by microbially generated heat (Finstein & Morris 1975), it is necessary that adequate material is present to facilitate heat buildup. Almost all heat generation is a result of microbial metabolism of organic substrates (Finstein & Morris 1975). All microorganisms have an optimum temperature for metabolic activity, and any deviation is manifested by a decline in growth and activity (Golueke 1972). Although a uniform temperature does not prevail throughout the mass of the composting material, it is important that core temperatures are greater than 55 °C, as this temperature range permits the most efficient rate of decomposition (Golueke 1972).

Chemical and Physical Aspects of Compost

Temperature

Temperature is the dominant parameter that controls microbial activity during composting (McKinley et al. 1985). There are three phases which occur through time: an initial phase, a thermophilic phase, and a curing or stabilization phase (Cook & Zentmyer 1986). The initial phase of composting, usually lasting 1-2 days, is a period of rapid temperature increase during which temperatures rise from ambient to 40 or 45 °C (Cook & Zentmyer 1986). Accumulation of microbial heat is at first stimulatory to developing mesophilic microorganisms, up to 35 °C, but this rate of increase diminishes and reaches a plateau from 35 to 55 °C (Cook & Zentmyer 1986; Finstein & Morris 1975). Although temperature is a critical parameter governing composting, the physical and chemical environment surrounding the microbes is constantly changing, primarily as a result of accumulation of metabolic products (Ciavatta et al. 1993). The metabolic heat produced by microorganisms increases the temperature of the composting pile to 70 or 80 °C. As the process nears completion, decomposition rates slow and temperature returns to ambient. In the first phase of composting, degradation of sugars and proteins by the mesophilic microbial community results in increased CO₂ production and an increase in temperature and depleted substrates (Hellmann et al. 1997). As temperatures reach 40-45°C, the second or thermophilic stage commences during which temperatures rise to 70 °C. It is during this stage that weed seeds and pathogens present in the compost are

killed, and the majority of cellulose, hemicellulose and lignins are degraded (Cook & Zentmyer 1986).

Although most labile components are decomposed, refractory components remain intact (Horwath & Elliott 1996). Heat buildup becomes inhibitory to many microbes as temperatures reach \geq 70 °C (Golueke 1972). Methane (CH₄) production increases during high temperature and low redox conditions as a result of thermophilic, methane-producing bacteria (Hellmann et al. 1997). This initial heat increase parallels the expansion, stagnation and collapse of the mesophilic microbial community (Finstein et al. 1983). As temperatures decline, the third or curing and stabilization phase commences, during which mesophiles re-colonize the pile and decomposition continues. Temperature declines as readily available substrates become exhausted (Finstein & Morris 1975). As temperatures decline, biomass decreases by up to 95% compared to initial, methane production decreases, and N2O production increases (Hellmann et al. 1997). Breakdown of recalcitrant components is mediated by a shift in microbial community function, to cellulose, hemicellulose and lignin decomposers (Horwath & Elliott 1996). Actinomycetes remain, fungi reappear, and cellulose-degrading bacteria appear (Herrmann & Shann 1993).

Aeration

Aeration is an important factor in the efficiency of decomposition. In the absence of a ventilation system for compost, oxygen often becomes a limiting factor and reduces the rate of decomposition (Finstein et al. 1983; Itavaara et al. 1997). Air requirements of microorganisms depend on the type of waste (e.g. nutrients, particle size) the process temperature, the stage of the process (e.g. initial, thermophilic, or stabilization) and the process conditions (e.g. moisture content, structures, etc.) (Stentiford 1996). The main products of aerobic decomposition include ammonia, CO₂, water, heat and humus (Cook & Zentmyer 1986). The majority of composting occurs in the outer oxygenated zone, while the inner zone may undergo anaerobic decomposition (Finstein et al. 1983). Anaerobic products include the fermentation products methane, CO₂, and intermediates such as organic acids and alcohols (Cook & Zentmyer 1986).

Several commonly used aeration methods include natural, passive, and forced aeration (Sartaj *et al.* 1995). Natural aeration is the natural diffusion of warm air upward which draws ambient air into the base of the compost pile. The path of ambient air entering the sides of the composting pile and leaving through the top is a result of high internal temperatures, and is referred to as a 'Chimney effect' (Hellmann *et al.* 1997). The disadvantage of natural aeration is the inability to readily change the physical conditions within the pile mass (Stentiford 1996). Windrow compost systems are the most commonly used forms of natural aeration. Long rows of compost are usually aerated periodically by turning the piles with machinery. Passive aeration involves a means of accelerated air movement by placing objects, usually perforated pipes at the base of the piles (Sartaj *et al.* 1995). This method increased the rate of composting over that of natural aeration although the influence zone of the pipes was limited to the interior and bottom half of the pile (Sartaj *et al.* 1995). As air diffusing throughout the pile is not uniform, uneven composting can be an undesired result (Golueke 1972).

With forced aeration, air is actively pushed into the pile, and is most commonly used with a closed or invessel composting system. This closed system is designed to maximize the rate of microbial decomposition and optimize temperature and moisture via ventilation (Finstein *et al.* 1983; Golueke 1972). This costly method is feasible when used for feedstocks that could potentially be health or industrial hazards including sewage sludge and toxic materials. However, forced aeration has been successfully used on static piles, demonstrating a high degree of process control with rapid rates of decomposition (Sesay *et al.* 1997). In some cases, forced aeration has led to desiccation and resultantly slow rates of desication in windrow compositing (Itavaara *et al.* 1997).

Moisture

Another component important to the composting process is moisture. Hoitink and Kuter (1986) stated that the optimum moisture content (on a wet weight basis) for composting varies with feedstocks, but ranges from 60 to 70%. Moisture gains and losses are related to aeration and temperature beause water is a product of aerobic respiration and evaporation is a function of exposure to air currents and temperature (Finstein & Morris 1975). The main mechanism of heat removal (~90%) in an aerated static pile system is water evaporation (Sesay *et al.* 1997). Water contents that facilitate or result in the drainage of water from the base of the pile will restrict airflow and create low oxygen tensions (Hoitink & Kuter 1986).

The effect of moisture and aeration can explain a portion of the initial composting process. Under adequate aeration, the temperature increase in composting piles is short due to a period of intense microbial heat generation at the expense of organic waste. With adequate aeration, the microbial generation of heat drives vaporization, resulting in a system that tends to become water-limited (Finstein et al. 1983). Although moisture contents less than 45-50% are limiting, water matric potentials less than 35% (on a weight basis) reduce microbial activity (Golueke 1972; Frost et al. 1992). The minimum moisture level at which bacterial activity occurs is 12-15% (Golueke 1972). In the curing or stabilization phase, composts that contain bark as a feedstock still have large surface areas of woodchips remaining, which promote microbial activity and result in increased heat output and drying (Hoitink & Kuter 1986). Since fungi are the primary colonizers as compost piles dry, fungal biomass provides a source of nutrients for the rapidly expanding bacterial population that occurs when water is added to the system (Frost *et al.* 1992). Dry composts (<34% moisture) colonized primarily by fungi were found to be conducive to *Pythium* diseases (Hoitink *et al.* 1997b). To induce plant disease suppression, Hoitink *et al.* (1997b) suggests that moisture content must be high enough (at least 40–50% w/w) to allow bacterial and fungal colonization of the substrate after peak heating.

Carbon:nitrogen ratio, (C:N)

The C:N ratio is important in the nutrient balance and, thus, the decomposition rate and end uses of a compost pile. The optimum starting C:N ratio ranges between 20:1 and 25:1 (Golueke 1972). During the composting process, carbon is lost as CO2 which progressively narrows the C:N ratio (Finstein & Morris 1975). This is normally true except for an occasional C:N ratio increase due to loss of ammonia from some systems (Mathur et al. 1993). Although there are many intermediates and side reactions, the general breakdown sequence of protein is into peptides, amino acids, ammonium compounds and, finally, incorporation into bacterial protoplasm, or release as atmospheric nitrogen or ammonia (Golueke 1972). Carbon is broken down from carbohydrates to simple sugars, organic acids and into end products of CO₂, and incorporation into bacterial protoplasm (Golueke 1972). The C:N ratio is closely related to volatile solids because, as material composts, carbonaceous material is mineralized while nitrogen content remains relatively constant. High NH_{4}^{+} levels are considered indicative of unstable organic matter (Zucconi et al. 1981). Normally, most available N is converted to stable forms that resist further ammonification.

When the C:N ratio is low, there is not enough carbon. Nitrogen may be lost to microbes through volatilization as ammonia into the atmosphere, producing an unpleasant odour (Finstein & Morris 1975). Alternatively, compost with an excessive C:N ratio has problems with slow, inefficient decomposition, requiring more time to complete (Seekins 1996). However, low or nitrogen-deficient composting may be beneficial in some situations, as it avoids the production of odours, which can also be accomplished by lowering moisture content (Finstein & Morris 1975).

The C:N ratio is an important factor in determining compost maturity and stability. An ideal C:N ratio of a mature compost is about 10:1, although sufficiently composted materials may fall within a range of 5:1 to 20:1, depending upon the feedstocks (Mathur *et al.* 1993). Because of this variability, C:N ratio should not be used as an absolute indicator of compost maturity (Hirai *et al.* 1983). However, as organic carbon to organic nitrogen ratios of water extracts of well-matured composts were almost always between 5:1 to 6:1 regardless of the type of raw materials, Hirai *et al.* (1983) concluded that this test may be a useful indicator of maturity. If immature compost with a high C:N ratio is applied to soil, the carbon levels cause nitrogen from the soil to be consumed in the continuation of decomposition. This immobilization of soil nitrogen into microbial biomass can impair plant growth as a result of a deficiency in the nitrogen supply (Barberis & Nappi 1996; Sesay *et al.* 1997; Forster *et al.* 1993). In contrast, slightly immature composts with low C:N ratios can cause a flushing of water-soluble material containing phytotoxic properties or carry high pollutant levels (Forster *et al.* 1993).

pH

Although variation is common in a compost pile, there is a general trend for pH to become acidic at the onset of decomposition, and then rise, reflecting the loss of organic acids through volatilization and mineral decomposition, and the release of ammonia through mineralization of organic nitrogen (Finstein & Morris 1975). The acidity of the initial material is a result of organic acids that are formed during fast degradation, which often occurs before the material is even in a composting pile (Hellmann et al. 1997). Composting increases pH from organic acid depletion, release of alkali ions, and the accumulation of ammonia (Hellmann et al. 1997). Acceptable pH ranges should be within tolerable levels to microorganisms, e.g. bacteria generally need a pH range of 6-7.5, fungi can generally tolerate a wider range, 5.5-8.0 (Golueke 1972), and actinomycetes, 5.0-9.0 (Goodfellow & Williams 1983). For fungi, the upper limit of pH is a function of the precipitation of essential nutrients from the medium, rather than pH itself (Golueke 1972). Hoitink and Kuter (1986) indicated the optimum pH range for decomposition is between 6.5 and 8.5. pH affects the potential for beneficial bacteria to colonize composts; below pH 5.0 bacterial biocontrol agents are inhibited (Hoitink et al. 1997b). When constructing a bark-containing compost pile, the low pH of bark materials (4.5-5.2) should be offset by the addition of ammonium nitrogen-containing materials, and/or poultry manure to increase pH (Hoitink & Kuter 1986). To curtail excessive ammonia loss, Hoitink & Kuter (1986) suggested that pH should be below 7.4 in aerated composting systems. pH is an important indicator of aeration levels within a composting pile. Well-aerated compost piles generally have a high pH, whereas piles with anaerobic conditions have decreased pH values (Jimenez & Garcia 1989).

Biological Aspects of Compost

Microorganisms

Microbial diversity is a prerequisite for a satisfactory composting process (Beffa *et al.* 1996b). A large variety of mesophilic, thermotolerant and thermophilic aerobic microorganisms (e.g. bacteria, actinomycetes, yeasts,

moulds, and fungi) are involved in the composting process (Beffa et al. 1996b). A high bacterial diversity of mesophilic bacteria appeared during the curing or maturing phase (e.g. nitrogen-fixers, producers of large amounts of extracellular polysaccharides). Their incorporation into soil increases fertility (e.g. nitrogen-fixers, nitrifiers, sulphur-oxidizers), structure (e.g. exopolysaccharide producers), and microbiology (Beffa et al. 1996b). Many factors determine the microbial community during composting but temperature is a major factor (Beffa et al. 1996b). Although temperature boundaries between mesophile and thermophile microbes are known, the exact division between them is not always distinct (Davis et al. 1992). Davis et al. (1992) demonstrated that many mesophiles can grow at 60 °C, and some even at 80 °C, while over half of the thermophilic isolates grew below 40 °C. Bacteria are present initially and throughout the process, fungi appear 7-10 days after the onset of composting, and actinomycetes are prevalent only in the final stages (Golueke 1972).

Bacteria

Eubacteria, or true bacteria, unlike fungi and actinomycetes thrive during all stages of composting. Bacteria constitute the majority of microorganisms in composting piles, with eubacteria and actinomycetes usually present in at least 100-fold greater numbers than fungi (Davis et al. 1992). Finstein & Morris (1975) noted the variety of cell shapes and sizes at low temperatures and a trend towards relative uniformity at higher temperatures. As the temperature approached 55 °C, rod-shaped bacteria disappeared, apparent sporeformers (e.g. longer rods) became more common, and spores became evident as temperatures rose above 55 °C (Finstein & Morris 1975). Extreme environments characteristically have relatively homogenous communities dominated by few species (Finstein & Morris 1975). Nakasaki et al. (1985b) found *Bacillus* spp. and *Azotobacter* spp. to be common mesophilic bacteria responsible for CO2 evolution at the early stage of composting when the temperature was <40 °C. Mesophilic microorganisms are partially killed or poorly active during the thermogenic stage (40-60 °C) (Beffa et al. 1996b). Colony variety decreased as temperature increased, with a shift from Pseudomonas, Achromobacter, Flavobacterium, Micrococcus and Bacillus to one dominated by Bacillus (Carlyle & Norman 1941). Bacteria related to B. schlegelii, Hydrogenobacter spp., and particularly to the genus Thermus (T. thermophilus, T. aquaticus) appear to be the main active microbes in hot composts $(65-80 \degree C)$ (Beffa et al. 1996b). Thermophilic isolates were found to be mainly gram-positive (86% of all tested), along with a lesser degree of mesophiles from later stages of composting to be 65.4% gram-positive (Davis et al. 1992). However, high numbers (e.g. $10^7 - 10^{10}$ cells/g dry wt.) of heterotrophic gram-negative (aerobic) thermophilic bacteria from the genus Thermus (non-sporeformers) grew

at temperatures >70 °C (Beffa *et al.* 1996a). Nakasaki *et al.* (1985) isolated a large number of mesophilic bacteria at the thermophilic stage of 60 °C, of which more than 60% were in the vegetative state. Bacterial survival in high-temperature composting material is possible through formation of microcolonies (Nakasaki *et al.* 1985b). Mesophiles are likely to contribute little to compost degradation at these temperatures (Nakasaki *et al.* 1985b).

Actinomycetes

Actinomycetes are a higher form of bacteria that are primarily strict aerobic saprophytes, and are common in many environments (Goodfellow & Williams 1983). Their ubiquity is a result of their ability to utilize a wide range of carbon sources and to sporulate prolifically (McCarthy & Williams 1992). Actinomycetes colonize more slowly than bacteria and fungi in compost and adhere to the substrate generally within 15.3 cm of a well-aerated compost surface (Lacey 1973). Colonization is minimal in areas that are poorly aerated. Actinomycetes can be seen as a white film on the surface of organic matter at a later period in the composting process (Nakasaki et al. 1985a). With an optimum growth between 25-30 °C and a pH of 5-9, these microorganisms are the most significant group of microbes in the degradation of relatively complex, recalcitrant polymers (Goodfellow & Williams 1983; McCarthy & Williams 1992). As actinomycetes develop more slowly than most bacteria or fungi, they are ineffective competitors when nutrient levels are high, but become more competitive as nutrient levels decrease (Nakasakiet al. 1985a). To facilitate the degradation of insoluble and polymeric carbon sources, actinomycetes secrete a range of extracellular enzymes (McCarthy & Williams 1992). Golueke (1972) found Actinomycetes thermophilus, Streptomyces and Micromonospora spp. to be common in compost. Although optimum growth temperatures fall in the mesophilic range, obligate thermophiles such as Thermoactinomycetes and Saccharomonospora spp. have been isolated (Goodfellow & Williams 1983). Certain species of actinomycetes are more tolerant to high temperatures, becoming increasingly active as temperatures approach and surpass 60 °C, when the levels of nutrients decrease (Nakasaki et al. 1985a).

Fungi

Lignocellulose, representing a large reservoir of carbon, is a complex polymeric substrate whose degradation involves activity of a range of hydrolytic and oxidative enzymes (McCarthy & Williams 1992). Fungi are regarded as the most important primary lignocellulose degraders (McCarthy & Williams 1992). Because lignin and cellulose are closely associated in lignocellulosic material, it has been postulated they are depolymerized simultaneously (Davis *et al.* 1992; Deschamps *et al.* 1981). Moisture content is critical to fungal involvement in decomposition; high water values generally favour bacteria over fungi (Finstein & Morris 1975). Nakasaki et al. (1985a) reported that fungi could barely be detected in certain cases, partly due to high moisture content of the composts. Although fungi are more often found on cool, dry compost exteriors, this can be misleading to their true nature (Finstein & Morris 1975). Fungi are killed or are present transiently as spores at temperatures >60 °C (Beffa et al. 1996b). Thermotolerant fungi have been reported to grow in a temperature range of 22.5 to 45 °C (Finstein & Morris 1975), and an optimum range between 45 and 50 °C (Nakasaki et al. 1985b). The disappearance of viable fungi is well advanced before temperatures reach 60 °C and essentially completed by 65 °C (Finstein & Morris 1975; Nakasaki et al. 1985b). Golueke (1972) found common species of fungi in composts to include Thermomyces spp., Penicillium duponti and Aspergillus fumigatus; while Geotrichum candidum, Mucor pusillus (mesophiles), and Cladosporium thermomycetes (thermophile) have also been found (Finstein & Morris 1975). Although it is known that a consortium of microorganisms may be necessary to degrade lignocellulosic material, interactions among species are not well documented (Davis et al. 1992).

Compost Maturity and Process Monitoring

The principal requirement for an organic material to be safely, conveniently and effectively used as a soil amendment is the degree of maturity, achieved after the treatment process (Beffa et al. 1996b; Senesi & Brunetti 1996). The identification of an accurate, simple means of estimating the maturity of organic matter would be beneficial because short-term effects of composts following application can be significant (Adani et al. 1995; Forster et al. 1993). A clear definition of maturity would allow more consistent evaluation of quality and stability of finished composts. A number of criteria based upon various physical and chemical indexes, enzymatic and microbiological tests, plant bioassays and physiochemical parameters have been proposed for evaluating the degree of maturity in the end product (Senesi & Brunetti 1996).

Methods for the evaluation of compost maturity continue to be debated. Chemical and biological stability of the end product seems to be very difficult to define with only a single analytical method (Beffa *et al.* 1996b). Although results have generally been successful with single batches, there has been variation in individual test results, among results from different tests, and among compost batches prepared from different feedstocks. There is no single method which can provide an accurate indication of compost maturity and stability (Barberis & Nappi 1996). In one study, no relationship was found between the results of single microbial methods and chemical data (Forster *et al.* 1993). Other researchers have also concluded that indices are only partially valid since they cannot be applied indiscriminately to all organic matrices (Ciavatta et al. 1990). Adani et al. (1995) found a high correlation between C:N ratio and the ligno-humic fraction, which is important because the C:N ratio was not correlated with microbial biomass or other physical-chemical parameters measured (McKinley et al. 1985). Many useful and reliable chemical parameters used to follow the evolution of different materials during the composting process are of no value if used in attempts to characterize and discriminate among composts of different origin and feedstock (Barberis & Nappi 1996). A number of these tests are documented in the following research papers: Zucconi et al. (1981), Chanyasak & Kubota (1981), Riffaldi et al. (1986; 1983), Zucconi & De Bertoldi (1987), Jimenez & Garcia (1989) and Barberis & Nappi 1996.

Wet, immature composting piles can induce anaerobic decomposition resulting in a release of toxic substances such as alcohol, methane and acetic acid (Senesi & Brunetti 1996). After harvest, immature composts can immobilize nitrogen, have fresh substrates, intermediates, phytopathogenic characteristics, and unacceptable pollutant levels (Forster *et al.* 1993).

Selected lipid or carbohydrate fractions in soil organic matter that are less biodegradable can serve as indicators of the degree of development of organic matter (Dinel et al. 1996; Insam et al. 1996). As a result, a more recent parameter for definition of mature composts uses increasing amounts of relatively bioresistant organic components (Dinel et al. 1996). Changes in lipid fractions of composts and examination of biodegradability of diethyl ether (DEE) extractable lipids and bioresistance of chloroform (CHCl₃)-extractable lipids has found that decomposition of organic matter yields increasing amounts of long chain aliphatic (lipid) compounds and decreasing amounts of polysaccharide materials (Dinel et al. 1996). It was concluded that lipids became more homogeneous during composting. Microbial communities in older compost use an increasing number of carbohydrate substrates (e.g. lactulose, lactose, erythritol, β -methyglucoside, sorbitol, turanose) than communities of younger composts (Insam et al. 1996). Biolog (Biolog, Hayward, CA, USA) microplates have been used to show that biomass and basal respiration decrease with compost age due to a decrease in substrate availability (Insam et al. 1996).

Researchers have stressed the necessity of simplification of analytical methods for maturity determination before incorporation into routine monitoring. Many technologies which are of interest to understanding the maturation process seem too sophisticated and expensive to serve as routine monitoring tools in small- or medium-sized composting plants.

Evaluation of Microbial Activity as a Measure of Maturity

Studies on changes of chemical processes in composts are extensive, but information on biological and microbial processes are less common (Insam *et al.* 1996). Because physical and chemical parameters are subject to a greater degree of variability, their use in evaluating or estimating biological activity is debatable (Richard & Zimmerman 1995). Distinct microbiological features, however, might provide information on the stability of composted materials (Forster *et al.* 1993). Because microbial community structure and temporal dynamics can change in response to environmental influences, studying these interactions can be invaluable in understanding ecosystem functioning (Garland 1997) and improving the efficiency and quality of the composting process and its products (Herrmann & Shann 1997).

Since decomposition is linked to microbial activity, respiration may be the best method for determining activity and stability (Adani et al. 1997). Because respiration rate is independent of the initial feedstock characteristics, it should provide an indication of microbial activity and reflect the degree of stabilization in open or closed composting systems (Iannotti et al. 1993; Richard & Zimmerman 1995). Microbial respiration is affected by moisture, temperature, oxygen and nitrogen availability (Herrmann & Shann 1993). Measurements of microbial respiration can be problematic as they are subject to environmental constraints aside from changes in carbon substrates characteristic of the decomposition process. CO₂ evolution can also be used for studying microbial activity because photosynthesis is virtually negligible in the composting process (Itavaara et al. 1997). Another indicator of activity is N₂O, a by-product of nitrification and denitrification. N₂O was produced only during the first four days of composting while temperatures were low, and after the thermophilic stage during declining temperatures (Hellmann et al. 1997). Methane (CH_4) is a trace gas emitted during the process of methanogenesis and can be used to estimate the level of anaerobic decomposition (Hellmann et al. 1997).

As composting is dependent on microorganisms, measuring levels of microbes and changes in functional communities should be an integral part of monitoring (Insam et al. 1996). Determining roles of microorganisms involved in composting could be used for process improvement (Golueke 1972). Microbial ratio indexes may be used as criteria for evaluating the level of compost activity and maturity (Kostov et al. 1994). Because degradation of complex molecules by microbial consortia is more efficient than by microbes in isolation, changes in microbial activities during composting have been measured (Atkinson et al. 1997). Although enumeration of microbes is a commonly suggested approach to estimating community characteristics and dynamics, most methods are not satisfactory. Serial dilutions and spread plating on media are known to underestimate the total number of microbes, partially because of unculturable microorganisms (Chung & Neethling 1988; Palmisano et al. 1993). In addition, single colonies on plates may arise from several bacterial aggregates (Tunlid et al. 1989). The isolation and description of various compost microorganisms may

not be useful as it is unlikely that any particular organism could be the chief agent of decomposition throughout the variable conditions of composting (Herrmann & Shann 1997).

To date, the most effective parameters for measuring compost stability reflect the level of microbial activity (Richard & Zimmerman 1995). Phospholipid phosphate, however, may provide an accurate measure of microbial biomass as it is rapidly destroyed after cells die and, therefore, is a good indication of the amount of living microbial biomass (McKinley et al. 1985). Community level approaches based on analysis of biochemicals such as phospholipid fatty acid analysis (PLFA). DNA or RNA, eliminate the bias involved in culturing of microbes (Garland 1997). In an earlier study, alkaline phosphatase, acid phosphatase, endo-cellulase, glucosidase, and lipase were measured to identify community structure (Herrmann & Shann 1993). Cellulase activity, measured with endo-cellulase and glucosidase peaked towards the end of curing where utilization of more recalcitrant nutritional sources (e.g. cellulose, lignocellulose, lignins) was common (Herrmann & Shann 1993). Increased cellulase activity, caused by a shift in community structure towards cellulytic fungi and bacteria, was a good indicator of stability but not necessarily maturity, as this only indicated that simple organic substrates were depleted. It was concluded that enzymatic methods indirectly reflect the activity of the microbial community and substrates being utilized (Herrmann & Shann 1993). Community patterns of sole carbon source utilization have been used to study microbial community dynamics, using the Biolog microtitre plates (Garland 1997). Biolog plates use redox dyes to identify bacterial isolates as well as metabolic traits which could lead to identification of functionally relevant characteristics of communities (Garland 1997). However, the majority of isolates tested have not matched with the Biolog database (Atkinson et al. 1997). Some variables in microplates used for functional characterization of communities may be a result of the culturable fraction being higher due to cooperative effects between actively growing microbes and those with the inability to grow on solid media, the culturable fraction being lower as a result of antagonistic interactions among microorganisms, or toxic effects of redox dyes (Garland 1997).

Phospholipid fatty acid (PLFA) analysis has been used to ascertain changes in microbial composition during composting by describing functional and physiological diversity and structure in communities (Herrmann & Shann 1997; Bossio *et al.* 1998; Carpenter-Boggs *et al.* 1998). To relate the complex mixture of PLFA back to the organisms present, a structure group interpretation is employed. In some cases fatty acid biomarkers have been identified for particular organisms (Figure 1, Table 1). Since PLFA are rapidly broken down, they are a useful measure of the current community of microbes (Carpenter-Boggs *et al.* 1998). As PLFA profiles are characteristic of certain microbes



Figure 1. Diversity and succession of microbial communities in compost as determined by PLFA analysis. Day 0 = start of composting, samples were taken on day 200 (sample 1), day 230 (sample 2), and day 306 (sample 3), with day 306 being the date of compost completion. Microbial Insights Inc., Knoxville, TN (www.microbe.com) conducted PLFA analysis.

Table 1. Phospholipid fatty acid (PLFA) structure groups and general classification of associated bacteria.

| PLFA structure group | General classification |
|---|---|
| Monoenoics (Monos) | Found in Gram negative bacteria, which are fast growing, utilize many carbon sources, and adapt quickly to a variety of environments. |
| Terminally Branched Saturated (TerBrSats) | Representative of Gram positive bacteria but may also be found in the cell membranes of some Gram negative bacteria. |
| Branched Monoenoic (BrMonos) | Commonly found in the cell membranes of obligate anaerobes such as sulfate or iron reducing bacteria. |
| Mid-Chain Branched Saturated (MidBrSats) | Common in Actinomycete spp., sulfate reducing bacteria and certain Gram positive bacteria. |
| Normal Saturated (Nsats) | Found in both the prokaryotic and eukaryotic kingdoms. |
| Eukaryotes (Polys) | Found in organisms such as fungi, protozoa, algae, higher plants and animals. |

associated with particular stages in the composting process and temperature range, their presence/absence was used to define microbial communities present in various stages of composting (Herrmann & Shann 1997). This data allows for real time evaluation of compost processing and maturity, as it follows general patterns in the microbial community composition. Carpenter-Boggs *et al.* (1998) showed a distinct shift in the functional microbial community as composting progressed. The PLFA profile was found to discriminate clearly amongst microbial communities in different soils (Bossio *et al.* 1998).

Compost and the Suppression of Plant Disease

Benefits of compost use include a decrease in mass and volume of organic wastes along with associated land-filling problems, and nutrient and organic matter maintenance or restoration in soil systems (Adani *et al.* 1995; Insam *et al.* 1996; Sesay *et al.* 1997; Gomez 1998). Compost contributes to soil fertility, structure, porosity, organic matter, water-holding capacity, cation exchange capacity, and other aspects of a soil system (Zucconi

et al. 1981; Itavaara *et al.* 1997; Sesay *et al.* 1997). In addition to the above benefits, composts have been implicated in the suppression of a variety of plant diseases and associated pathogens. A number of articles have addressed this issue (Baker & Cook 1974; Lumsden *et al.* 1983; Hoitink & Fahy 1986; Hoitink & Kuter 1986; Hoitink *et al.* 1997a; Hoitink *et al.* 1997b; Whipps 1997a; Whipps 1997b).

Compost and the suppression of turfgrass diseases

There is increased interest in the potential benefits of using compost in turfgrass establishment and management. Reasons for this interest include the ability of composts to increase nutrient retention and availability, cation exchange capacity, and humic components that serve as a source of organic matter (Sesay *et al.* 1997) and contribute to soil fertility and structure, porosity, and water-holding capacity (Zucconi *et al.* 1981; Itavaara *et al.* 1997; Sesay *et al.* 1997). The use of compost for disease suppression in turf is a more recently established alternative use of compost. Interest in biological forms of control of pathogens has increased due to concern over pesticide use, occurrence of pesticide resistance in some pathogens and lack of chemical controls or resistant plant varieties (Whipps 1997a). Naturally suppressive (antagonistic) composts can be incorporated into normal golf course maintenance by replacing sphagnum peat or other organic materials currently used in topdressing mixtures. Topdressings are applied primarily to smooth putting surfaces and to manage thatch accumulation (Nelson & Craft 1992). Compared to peat, compost provides quicker greening of turfgrass, a more dense stand, reduction of thatch, increased earthworm activity and especially increased microbial activity (Block 1997). Another reason for replacing peat is that this material is a non-renewable resource from ecologically fragile zones described as 'the most delicate areas of interaction of vegetation and hydrology on the planet' (Underwood 1992). Covering 3% of the Earth's surface, these peat bogs and fens are crucial to the world's biosphere, and are considered to be as important as tropical rainforests (Underwood 1992).

Common diseases of turfgrass include dollar spot (Sclerotinia homoeocarpa), Pythium spp., and snow mould (Typhula ishikariensis, Typhula incarnata, Micro-dochium nivale).

Dollar spot

Dollar spot, caused by Sclerotinia homoeocarpa F.T. Bennett, is the most commonly occurring turfgrass disease in North America (Couch 1995). More money is spent on control of dollar spot than any other turf disease of golf courses (Goodman & Burpee 1991). Symptoms include the appearance of yellow-green blotches that progress from a water-soaked appearance to a bleached or tan colour with reddish brown borders (Couch 1995; Smiley et al. 1992). Early morning mycelium may be visible on sunken, circular patches that range in size from a few blades of grass up to 5-7.5 cm in diameter (Couch 1995). S. homoeocarpa is infective from late spring to early autumn, when temperatures range between 15–30 $^\circ C$ and humid nights result in heavy dew (Smiley et al. 1992; Couch 1995). Peak growth occurs between 21–27 °C when humidity is 85% or greater (Couch 1995).

Cultural controls other than the use of fungicides include the encouragement of plant growth with nitrogen applications leading to more frequent mowing which removes necrotic and infected tissues, thorough but infrequent watering which holds soil near field capacity (-0.033 MPa) and reduces moisture-stressed susceptibility of turfgrasses to disease, and avoidance or removal of dew and guttation water from turf (Smiley *et al.* 1992; Couch 1995).

Pythium diseases

There is a spectrum of diseases caused by *Pythium* spp. which can be divided into foliar blights, crown and root rots, seed rots and damping-off (Nelson & Craft 1991a; Smiley *et al.* 1992). Two common diseases that occur on

established golf course greens are Pythium blight and Pythium root and crown diseases. Symptoms may occur in all weathers, but are most obvious and recognized in hot, humid weather (29–35 °C, RH \ge 90%) when damage to foliage is severe (Smiley *et al.* 1992; Couch 1995). All parts of the turfgrass plant are subject to attack, and symptom expression is related to the site of infection (Smiley *et al.* 1992).

Pythium blight, referring to species that cause foliar diseases of turfgrasses, can result in complete loss of foliage within 24 h of initial symptom appearance (Couch 1995). Pythium species that are involved include *Pythium aphanidermatum* Drechsler, *P. graminicola* Subrum, *P. arrhenamanes* Drechsler, *P. myriotylum* Drechsler, and *P. ultimum* Trow (Couch 1995). Small (2.5–10 cm), irregularly shaped purplish areas can appear under high humidity or in early morning when white, cobweb-like mycelium may be visible on leaves, which eventually develop into a water-soaked appearance (Smiley *et al.* 1992; Couch 1995). These lesions, which develop into light to reddish brown areas, are similar to symptoms of dollar spot.

Pythium-incited root and crown diseases are responsible for a general decline of turfgrass, usually with non-specific symptoms (Smiley et al. 1992; Couch 1995). Species pathogenic to roots and crowns include P. aphanidermatum, P. aristosporum, P. graminicola, P. arrhenomanes, P. irregulare, P. myriotylum, P. tardecrescens, P. torulosum, P. ultimum, and P. vanterpoolii (Couch 1995). Infected turf may appear thin and grow slowly while leaves may appear pale green to brown (Smiley et al. 1992; Couch 1995). Unlike Pythium blight, no foliar mycelium is present, making the disease difficult to diagnose (Smiley et al. 1992).

Effective water management, which includes increasing drainage, dew and guttation water removal, and avoidance of over-watering and leaf wetness duration are important cultural controls. In addition, trees and other foliage may be pruned to promote light penetration and air circulation and avoid local pockets of still, humid air (Smiley *et al.* 1992). The maintenance of slowrelease nitrogen fertilizer applications without overfertilizing, acid soil conditions, and avoidance of mowing in hot, humid weather will also decrease disease incidence (Smiley *et al.* 1992; Couch 1995). Fungicides are often used for control of *Pythium* spp. diseases, but are variable in efficacy on crown and root rot problems (Smiley *et al.* 1992).

Snow mould

Typhula blight, and Fusarium patch are two snow mould diseases that can result in serious damage to turfgrasses (Smiley *et al.* 1992).

Typhula Blight

Typhula blight, caused by the two fungal species, *Typhula ishikariensis* and *T. incarnata* Lasch ex. Fr.

[Typhula itoana Imai] is also called grey or speckled snow mould because of the characteristic white or greywhite mycelial mat that is speckled with numerous sclerotia on, or in, infected leaves (Smiley et al. 1992). T. ishikariensis is usually associated with the development of typhula blight where winters are longer and more harsh, having more than 90 days of continuous snow cover, than is the case with T. incarnata (Smith 1980; Lawton & Burpee 1990). T. ishikariensis outbreaks are generally more severe than those caused by T. incarnata. Although it may not be more pathogenic, the greater severity of T. ishikariensis is probably a result of an increase in turfgrass susceptibility, primarily a result of increased depletion of its energy resources due to the long snow cover period (Smith 1987). Symptoms appear as light yellow discoloured areas 2.5-7 cm in diameter with individual leaves progressing from a scalded, discoloured appearance to reddish-white and matted (Couch 1995). Typhula blight commonly develops in cold, wet weather and is usually more severe when turf is snow covered or heavily mulched for an extended period of time. Snow cover prevents soil from freezing and creates areas of high atmospheric humidity and relatively warm air temperatures of 2-5°C (Smiley et al. 1992; Couch 1995). Mild cases may occur where there is little or no snow, but severe outbreaks require persistent snow cover (Couch 1995).

Although fungicides are normally useful as preventative measures in the autumn, they are usually not effective when applied as curatives in late winter or early spring (Smiley et al. 1992). Cultural practices include construction of snow fences and planting of windbreaks to minimize snow accumulation as well as avoidance of snow compaction. Heavy applications of nitrogen late in the fall should be avoided but, in areas of low soil fertility, moderate slow-release fertilizer applications will promote more rapid plant regrowth in the spring (Smiley et al. 1992; Couch 1995). Turf should be managed to maintain thatch <1.3 cm and mowed into late autumn to insure that snow does not fall on a tall canopy (Smiley et al. 1992; Couch 1995). In the spring, disease-prone areas should be rapidly dried by removing snow and providing good drainage (Smiley et al. 1992).

Fusarium Patch

Fusarium patch, formerly known as pink snow mould, is the most commonly occurring low-temperature disease of cool season turfgrasses in many areas (Couch 1995). Fusarium patch is caused by *Microdochium nivale* Fr. Samuels and Hallett (teleomorph *Monographella nivalis* (Schaffnit) E. Müller). Former names have included *Fusarium nivale* ces. ex Berl. and Voglino and *Gerlachia nivalis* (Ces. Ex Berl. and Voglino) W. Gams and E. Müller. Previously, the name pink snow mould was used to describe the disease associated with snow melt, whereas fusarium patch was used to name the disease when it occurs without snow cover (Smiley *et al.* 1992). Although snow cover is not a requirement, the disease develops under cool, humid conditions that are most severe when heavily thatched turf is growing slowly, common from late fall to early spring (Smiley et al. 1992; Couch 1995). Symptoms first appear as small, water-soaked spots up to 7.5 cm in diameter, which are reddish-brown to tan-coloured in the centre, bordered by white or dull pink mycelium on the developing edges (Couch 1995). Optimal conditions for growth include high humidity and air temperatures from 0 to 7 °C which generally occur under deep, persistent snow on unfrozen ground, alternate thawing and snow cover, repeated frosts, or heavy mulches (Smiley et al. 1992; Couch 1995). However, outbreaks can occur at temperatures up to 18 °C in conditions of extended leaf wetness caused by ground fogs, mists, or frequent light rain showers (Smith 1987). The fungus ceases to be pathogenic at 21 °C (Smith 1987).

Common management practices for Fusarium patch are similar to those used for Typhula blight (Smiley *et al.* 1992). High applications of nitrogen fertilizer late in the season that promote succulent grass are particularly conducive to Fusarium patch, along with poor drainage and long leaf blades, which become matted (Smiley *et al.* 1992). Maintenance of low soil pH is an additional practice employed for control (Smiley *et al.* 1992).

Compost and Disease Suppression

Methods for control of disease: specific vs. general

Alternative methods for suppression of plant disease can be classified as either inoculants for biological disease control (specific, direct), or natural (general, indirect) suppression (Fokkema 1993; Whipps 1997b; Lucas 1998). Specific suppression is the introduction or inoculation of a single species or narrow group of microorganisms able to suppress activity of the pathogen (Nelson 1992; Hoitink et al. 1997b; Lucas 1998). This refers to the direct antagonistic effect of one organism on another, such as is the case with T. hamatum and T. harzianum (Lo et al. 1996). In this review, biological control is defined as any conditions under which, or practice whereby, survival or activity of a pathogen is reduced through the agency of any other living organisms (except humans), resulting in reduction in incidence of disease caused by the pathogen (Garrett 1965). Although the number of commercially available agents for control of soil-borne pathogens is still small, their development and potential use have received considerable attention over the last decade (Whipps 1997b). Methods of employing biological control agents for management of disease are related by the source and specificity of the organisms involved. Aside from a need for an improved understanding of microbial community functions, the complex microbial interactions involved in biological control add to the difficulties in determining exact mechanisms of suppression. Inconsistencies in the performance of biocontrol agents against pathogens is a concern. One explanation for this lack of consistency is the sensitivity of biocontrol mechanisms to fluctuations of environmental conditions to which they are exposed. (Dowling et al. 1996; Weller & Thomashow 1994). The use of combinations of biological agents has been suggested as a solution because incorporation of multiple control mechanisms may ensure that at least one will be functional under environmental conditions to which the biocontrol is exposed (Duffy et al. 1996). As a result, it seems logical that composts, having a diverse consortium of antagonistic microorganisms, would be an excellent choice for the study of biocontrol properties. Effective bacterial antagonists in compost include P. aeruginosa, P. fluorescens, P. putida, P. stutzeri, Xanthomonas maltophilia, Janthinobacterium lividum, Flavobacterium balustinum, Enterobacter cloacae, E. agglomerans, Bacillus cereus, B. mycoides, and B. subtilis (Hoitink & Fahy 1986). Of these species, F. balustinum and X. maltophilia were most effective in suppressing Rhizoctonia damping-off. Combinations of antagonists, such as T. hamatum and F. balustinum or X. maltophilia, were more effective in suppression than single antagonists.

General or indirect suppression of disease typically involves manipulation of the microbial balance by means of crop practices, cultural measures, and soil supplements such as composts (Lucas 1998). This type of suppression often may not provide complete control, but rather, may contribute to a reduction in occurrence and severity of pathogens and disease. Partial control will reduce use of chemical controls, and may also lower symptom severity below that of acceptable thresholds. General suppression is a method of controlling various pathogens without additional chemicals or organisms added to the media. This may occur naturally in diseasesuppressive soils, but is often produced through agricultural or horticultural practices which include use of organic amendments and composts (Whipps 1997a). Studies on microbial antagonism of soil-borne plant pathogens have shown that other soil microbes can have a large influence on the incidence and severity of disease (Lucas 1998). It is the general suppression of disease that is relevant to the use of composts as topdressings (Chen et al. 1988a; Inbar et al. 1991). Most control induced by compost is a result of microorganism activity in the rhizosphere, the area of soil immediately surrounding root surfaces (Hoitink et al. 1997b). There may be one or more factors contributing to disease suppression which can be divided into physiochemical characteristics and biological or microbial components (Figure 2) (Whipps 1997b). Physiochemical factors include physical and chemical aspects of the environment, whereas biological factors include microbially involved processes such as competition for nutrients (Chen et al. 1988b; Hoitink et al. 1993, 1997b; Lawton & Burpee 1990), antibiosis (Nelson 1992; Whipps 1997a), production of lytic and other extracellular enzymes and compounds (Ko & Lockwood 1970; Lockwood & Filonow 1981;

Lorito *et al.* 1994), parasitism (hyperparasitism and mycoparasitism) and predation (microarthropods e.g. springtails and mites) (Hoitink & Fahy 1986; Burpee *et al.* 1987), and host-mediated induction of resistance (Lucas 1998).

Examples and implicating issues surrounding biological control/suppression of turfgrass diseases with compost

There is a general uncertainty regarding the exact mechanisms by which suppression with composts is achieved. It is thought to be related to nutrient supply or other physiochemical characteristics of composts, microbial growth, activity and metabolism, or a combination of these factors. There are many examples of successful control of turfgrass disease without mention of mechanisms of control. Many researchers are in debate over the role of chemical and physical characteristics compared to that of resident microbial populations in compost.

The indirect role that increased levels of microorganisms in composts play in improving plant health and subsequent disease resistance has been studied. Microorganisms symbiotically form associations with plant roots, and increase availability of nutrients and production of plant growth stimulators (Nelson 1992). Competitive exclusion has been linked to the ability of microbes to colonize the rhizosphere successfully, during which, a microorganism is faced with a complex array of parameters such as water content, temperature, pH, soil types, composition of root exudates, mineral content, and other microbes. It is difficult to determine if colonization changes are a result of the direct effect of these parameters (O'Sullivan & O'Gara 1992). Disease suppression may also be due to enhanced microbial breakdown activity, resulting in an increased availability of nutrients, which may stimulate plants to more rapid recovery from disease. Through the use of composts, nutrient-dependent pathogens, such as Pythium spp. and Phytophthora spp., are inhibited through general suppression (Hoitink et al. 1993). In one study, based on a direct relationship between seed exudation and damping-off severity, it was concluded that the most important source of nutrients for development of populations of Pythium spp. was exudates from the host plant (Chen et al. 1988b).

Microbial populations are postulated to be the main direct mechanism by which composts suppress turf diseases. In a series of compost batches tested for suppression of Pythium damping-off, the batches containing the highest populations of heterotrophic fungi and antibiotic-producing actinomycetes were found to be the most suppressive (Craft & Nelson 1996). Suppression of *P. ultinum* was observed to increase with compost age and level of microbial activity (as measured by FDA hydrolysis) (Craft & Nelson 1996). The correlation of disease severity and hydrolysed FDA (fluorescein diacetate) indicated that microbial populations in the composts were major factors influencing



Figure 2. Suppression strategy for plant pathogens using either microbial inoculants or amendments.

disease suppression (Craft & Nelson 1996). Generally, microbial populations of fungi and actinomycetes were higher in suppressive than non-suppressive composts (Craft & Nelson 1996). Davis et al. (1992) noted many negative intermicrobial interactions in compost which included development of antifungal and antibacterial zones of inhibition on agar plates. Autoclaving of composted material destroyed or reduced suppressive effects on Pythium; suggesting microbial antagonists and their metabolites had an important role (Nelson & Craft 1992). Researchers have concluded that suppression of dollar spot was mainly due to microbial effects of the compost which appeared to directly interfere with pathogen growth and competition (Nelson 1991; Nelson & Craft 1992). B. subtilis, one of an estimated high concentration of disease suppressive bacteria in compost, was isolated from composted grass clippings from golf courses successful in biocontrol of Rhizoctonia solani, the causative agent of Rhizoctonia large-patch disease (Nakasaki et al. 1998).

Other examples of turfgrass disease suppression include general and specialty mixes of composts. On the North Shore Golf Course in Northfield, Illinios, an 80– 90% reduction in dollar spot was obtained with a late spring application of yard trimmings compost (Block 1997). The organic fertilizer Ringer Compost Plus (Ringer Corporation, 9959 Valley View Rd., Minneapolis, MN 55344, USA) provided substantially greater disease suppression than treatment with iprodione (Nelson & Craft 1991b). Sustane Turkey litter compost (Sustane Corporation, Cannon Falls, MN 55009, USA) provided some disease suppression while a topdressing mixture (30% compost, 70% sand v/v) of composted turkey litter and sewage sludge was inconsistent in suppression (Nelson & Craft 1992).

Chemical and physical characteristics, such as colour, fertilizer effects, and other factors have been implicated in the efficacy potential of compost to suppress disease. Researchers supporting this idea maintain that microbial populations in composts metabolically provide nutrients and other chemical compounds to plant hosts through the continual breakdown of composted material. A compost of yard trimmings did not prevent the occurrence of snow mould but did increase the recovery of grasses from disease in the spring (Block 1997). The author suggested that the dark colour of composted material increased radiant heat absorption, and naturally increased nutrient levels which stimulated growth (Block 1997). Although several bacterial and fungal species (Fusarium heterosporum, Acremonium spp., Rhizoctonia spp., Enterobacter cloacae, Pseudomonas fluorescens, P. lindbergii and others) have been highly suppressive to dollar spot, nitrogen application is still considered an implicating factor in control (Goodman & Burpee 1991; Hodges et al. 1994; Nelson 1991). Because nitrogen is a known cultural control method of dollar spot that aids turf in outgrowing the pathogen and promoting rapid recovery from disease, it is normally considered partially or even completely responsible for dollar spot control with composts and other natural organic fertilizers (Landschoot & McNitt 1997; Liu et al. 1995). However, nitrogen is also known to increase fungal and bacterial populations in turf and play a major role in microbial population dynamics (Liu et al. 1995). It is essential for the production of compounds involved in host resistance, including phenolics, phytoalexins, growth hormones, cellulose and carbohydrates (Huber 1980). The modes of action by which natural organic fertilizers suppress dollar spot are assumed to include increases in plant growth from nutrient availability, and increased microbial populations from those present in the fertilizers themselves, and/or those stimulated in turf through their application which may compete with or antagonize pathogens and protect plants from infection (Liu et al. 1995; Phae & Shoda 1990). Another suggested role of enteric bacteria in dollar spot suppression is the metabolic provision of nitrogen nutrition to turf (Nelson 1991).

Compost extracts

The use of compost extracts as a means of disease suppression is a rapidly developing area of investigation. Containing high levels of nutrients and varied microbial populations and metabolites, research has focused on the effects of compost extracts on pathogenic fungi and diseases (McQuilken et al. 1994; Weltzien 1991). In general, extracts are prepared by mixing compost at a 1:5 to 1:10 ratio with water and then filtering (through cheesecloth) to remove large particles after a specified incubation time. Extracts are then applied to plant materials (Weltzien 1991). Foliar sprays have shown potential for controlling a number of diseases, including downy and powdery mildews, potato late blight (Phytophthora infestans), Botrytis grey mould, anthracnose (Colletotrichum orbiculare) of cucumber (Cucumis sativus L.) and bacterial speck (Pseudomonas syringae pv. maculicola) of Arabidopsis thaliana (Stindt & Weltzien 1988; Trankner 1992; Weltzien 1989, 1991; Weltzien & Ketterer 1986; Zhang et al. 1998). The use of compost extracts to inhibit Botrytis cinerea Pers. Fr. has reached levels of 100% inhibition through direct inhibition of spore germination and mycelial growth (McQuilken

et al. 1994; Stindt 1990). Compost extracts provided control of downy grape mildew (Uncinula necator) equal to that of regular fungicide applications (Weltzien 1991). Suppression by extracts sterilized through filtration was significant, suggesting that an unidentified chemical factor played a role (Zhang et al. 1998). The ability of compost extracts to inhibit diseases was highly dependent on the presence of microorganisms, by comparison to the efficacy of heat-sterilized (autoclave, 40 min, 120 °C) extracts and stepwise elimination of microbes through membranes of decreasing pore sizes (Weltzien 1991). It was concluded that the number and quantity of living microbes in the extracts are largely, but not exclusively, responsible for disease suppression. Proposed mechanisms of suppression include direct inhibition, nutrient competition, induced resistance and disrupted communication between the pathogen and host (Weltzien 1991; Zhang et al. 1998). Compost water extracts have potential for biological control, especially in organic agricultural systems and low input agricultural systems in developing countries (McQuilken et al. 1994).

Physiochemical characteristics influencing disease suppression with composts

A variety of soil amendments have been developed to alter the soil environment such that specific pathogens are inhibited. Research in this area has focused on the use of composted softwood and hardwood tree barks that provide appropriate physiochemical characteristics for disease-suppression (Whipps 1997a). The diseasesuppressive properties of an organic amendment can be affected or altered by the physiochemical characteristics of the surrounding environment. These factors include media components that affect the abilities of certain pathogens to develop; such as clay, pH, exchangeable aluminum, nutrient levels (Ca, P, Mg), organic matter (Whipps 1997b), moisture, porosity and tillage practices (Henis & Chet 1975). The effects of these characteristics cannot be generalized upon as they have different effects in different environments (Whipps 1997a). Moisture may directly influence the pathogen, or indirectly affect pathogen development by modifying host symptoms, or by predisposing the host to infection (Henis & Chet 1975). Inorganic fertilizers and other elements can also affect disease through direct suppression of pathogens or indirectly by altering microbiological populations and host susceptibility (Henis & Chet 1975). A host plant may be able to grow at a pH unfavourable to disease development, or within ranges that favour activity of antagonistic microflora (Henis & Chet 1975).

Biological and microbial characteristics influencing disease suppression with composts

Mechanisms by which microorganisms suppress disease can be divided into several strategies. Suppressive microbes may act directly on pathogens through competition for seed, root or leaf exudates, antibiotic production, lysis, induction of host-mediated resistance in plants and parasitism of pathogens (e.g. microarthropods), although more generalized interactions can play an important role (Hoitink *et al.* 1997b). Successful disease suppression is more likely to involve combinations of these mechanisms. As a result, difficulties often arise when attempts are made to determine exact suppression mechanisms, especially with compost which represents a community structure rather than a single species.

Relationships among microbes can be positive or negative (Henis & Chet 1975). Although not classified into a specific mechanism of pathogen suppression, microorganisms can beneficially affect other microbes through general maintenance and life support processes. They may make nutrients available, synthesize and excrete nutrients (amino acids, vitamins), alter physical conditions optimal for growth, and decompose or neutralize toxic substances. Beneficial activities of microbes may stimulate plant growth directly through the production of plant growth hormones or through the production of natural chelators called siderophores that make iron available to plants (Hoitink et al. 1997b). However, microorganisms may also negatively affect each other through competition for nutrients, oxygen or space, or by excreting inhibitory metabolic products (Henis & Chet 1975; Whipps 1997a).

Compost-inhabiting microbes and suppression of plant diseases

Although exact mechanisms by which composts suppress turfgrass disease are generally unknown, a number of bacterial and fungal species have been identified that are known agents of control. One of the more costeffective methods of biological control of turfgrass diseases investigated involves the manipulation of natural populations of soil-borne microbes with applications of composted materials (Nelson 1992) (Hoitink & Kuter 1986). Knowledge of pathogen constraints imposed during dispersal, survival, early stages of infection or other stages where the pathogen is exposed to factors which may affect growth and viability will increase the effectiveness of biocontrols (Lucas 1998).

A miniaturized rapid bioassay was outlined for screening organisms to *P. aphanidermatum*, which causes Pythium blight of turfgrasses (Craft & Nelson 1992). The Tissue Culture Plate (TCP) assay involved mixing sterile sand, the potential suppressive bacteria in suspension, creeping bentgrass seed and *P. aphanidermatum* and rating disease development. This test was effective in screening large numbers of bacteria and identifying suppressive organisms within seven days. *E. cloacae* was found to be the most suppressive microorganism on *P. aphanidermatum* (Craft & Nelson 1992).

Trichoderma viride, a common inhabitant of compost, has been extensively studied and found to parasitize pathogens and suppress their growth in soil through production of antifungal antibiotics (Hoitink et al. 1997b). The mycoparasitic fungus, Trichoderma harzianum, can suppress fungal pathogens through the production of lytic enzymes (Geremia et al. 1993). Trichoderma harzianum (strain 1295-22) is a commercially available biological control agent able to control several plant pathogenic fungi, and can significantly reduce the severity of foliar symptoms of dollar spot, brown patch (Rhizoctonia solani), and pythium root rot (Pythium graminicola) when applied as a seed or soil treatment (Lo et al. 1996). Cell-wall degrading enzymes and mycoparasitism were implicated as control mechanisms (Lo et al. 1996). Both Trichoderma spp. (Hoitink et al. 1997b) and Penicillium spp. were predominant fungal parasites recovered from composts (Hadar & Gorodecki 1991). T. phacorrhiza is an effective biocontrol agent against Typhula blight, although it is dependant on an inoculation rate of 200 g/m³ (or $7.0 \times$ 10^3 cfu) to provide suppression equivalent to pentachloronitrobenzene (PNCB) (Lawton & Burpee 1990). T. phacorrhiza has been incorporated into alginate pellets for dispersal (Lawton & Burpee 1990). Competitive colonization of turfgrass thatch by T. phacorrhiza may be a factor in suppression of Typhula blight, along with competition for nutrients and/or space, or production of inhibitory compounds. Burpee et al. (1987) found that T. phacorrhiza was suppressive to T.i. var. ishikariensis through competition for nutrients rather than hyperparasitism or cellular lysis induced by an antibiotic or hyphal contact. They also postulated substrate competition and induced resistance as other antagonistic mechanisms.

Antibiotic-producing microbes may displace pathogens in soil and decaying plant residues such as turfgrass thatch (Nelson 1992). Antibiotic production by fluorescent pseudomonads was an important mechanism mediating pathogen suppression (Shanahan et al. 1992; You & Sivasithamparam 1994). Fluorescent pseudomonads belonging to the Pseudomonas putida-fluorescens group suppressed Ophiobolus patch (Gaeumannomyces graminis var. avenae) in Agrostis turfgrass through siderophore production (Thomashow & Weller 1988). The use of pseudomonads to suppress diseases in the field would involve initial fumigation of turfgrass greens, probably with methyl bromide, before introducing the antagonists, which would presumably dominate the rhizosphere as a result of their rapid colonization of fumigated soils (Wong & Baker 1984). Physiological activity of P. fluorescens involving the production of antibiotics, vitamins and auxins in guttation fluid of grasses led to inhibition of Sclerotinia homoeocarpa. In the same study, P. lindbergii was found to produce an undescribed antifungal antibiotic (Hodges et al. 1994). Bacillus species and their antibiotics isolated from composts are known to have antifungal activity against phytopathogenic fungi (Phae et al. 1990; Walker et al. 1998). Bark compost inoculated with Bacillus subtilis was found to be suppressive to Fusarium oxysporum f.sp. cucumerinum, Pythium ultimum, Verticillium dahliae,

Pyricularia oryzae, and *Rhizoctonia solani* through production of the extracellular antibiotic itvirin (Phae & Shoda 1990). In further studies, it was noted that different isolates of *B. subtilis* showed different degrees of suppressiveness although rapid growth was a common phenomenon (Phae *et al.* 1990).

Enterobacter cloacae was studied for control of dollar spot by applying antagonistic strains in a cornmeal-sand mix as topdressing on creeping bentgrass (Nelson 1991). E. cloacae population levels remained at 10^8 – 10^9 cfu/g after application, possibly a result of its apparent affinity for members of the Gramineae. Mechanisms of dollar spot suppression may be related to the observed adherence of E. cloacae to hyphae of similar fungi such as S. sclerotiorium (Lib.) de Bary, thus, directly interfering in pathogen growth and infection (Nelson 1991). Of the microorganisms tested, four potential antagonists were found to suppress S. homoeocarpa growth by 25-90% (Goodman & Burpee 1991). Production of compound toxic to S. homoeocarpa was a suggested mode of action because autoclaving the mix containing the antagonistic fungus, Fusarium heterosporum, resulted in only a 25% increase in dollar spot incidence (Goodman & Burpee 1991).

Mechanisms of Action - Disease Suppression

Compost may increase microbial activity which can suppress disease through one or a combination of physiochemical and biological characteristics which include: competition for nutrients, antibiosis, lytic and other extracellular cell wall-degrading enzymes, parasitism and predation and host-mediated induction of resistance.

Nutrient competition

Disease propagules are prevented from germinating by high microbial activity in composts through competition for nutrients (Hoitink *et al.* 1993). Craft & Nelson (1996) postulated that suppression is a result of elevated microbial activity resulting in increased competition with pathogens for root exudate components essential for pathogen germination and growth. Through continual removal of nutrients, especially carbon and iron (Whipps 1997a), pathogens are prevented from germinating and so remain inactive (Logsdon 1990; Nelson & Craft 1992). Alternatively, dormant propagules such as sclerotia, chlamydiospores and oospores may be stimulated to germinate but are unable to compete with active saprotrophic microbiota and are subject to nutrient stress, leading to lysis due to starvation.

Because soil-inhabiting pseudomonads produce fluorescent siderophores which have a high affinity for binding ferric iron, the unavailability of this nutrient may restrict growth and prevent germination of deleterious microorganisms (O'Sullivan & O'Gara 1992). As a result, fluorescent siderophores active in iron chelation have been implicated as an important mechanism in pathogen suppression (You & Sivasithamparam 1994).

Chen *et al.* (1988b) found that samples taken from the low-temperature edge of compost piles (cured 4 months) were suppressive to cucumber-damping-off caused by *Pythium ultimum*, while material removed from the higher-temperature centre or core was conducive to disease. The microorganism populations in the low-temperature area were taking up nutrients and creating a nutrient sink. This nutrient sink was the principal mechanism of suppression proven through destruction of the suppressive effect by the addition of nutrients to the compost, and the presence of higher nutrient concentrations in the conducive media (Chen *et al.* 1988b).

Complete autolysis of hyphae under conditions of nutrient deprivation imposed by microbial activity indicated that autolytic enzymes in mycelia are rapidly activated in hyphae exposed to low nutrient levels (Ko & Lockwood 1970; Lockwood & Filonow 1981). Several actinomycete species have been shown to cause complete lysis of living fungal mycelium, presumably through nutrient competition (Ko & Lockwood 1970). Burpee et al. (1987) found T. phacorrhiza was suppressive to T.i. var. ishikariensis, the causative agent of typhula blight, through competition for nutrients, substrate competition and induced resistance, rather than hyperparasitism or cellular lysis induced by an antibiotic or hyphal contact. Microbes inhabiting the plant tissue surfaces served as biological buffer zones, thus preventing the pathogen from infecting (Baker & Snyder 1965). In general, populations of fungi and actinomycetes were higher in suppressive then non-suppressive composts (Craft & Nelson 1996). There are a number of examples where nutrient competition has been a factor in suppression of plant pathogens (Chen et al. 1988b; Lawton & Burpee 1990; Di Pietro et al. 1992; O'Sullivan & O'Gara 1992; Hoitink et al. 1993; Craft & Nelson 1996; Whipps 1997a; Van Dijk & Nelson 1998; Lucas 1998).

Antibiosis

Another mechanism of biocontrol involves antibiosis, the inhibition of one organism by a metabolite of another (Baker & Cook 1974). Biological control effects mediated through antibiotic production may be a survival or competitive mechanism which evolved within the soil microbial population (Whipps 1997a). Antibiotics are often secondary metabolites produced by antagonists when nutrients become limiting and are frequently of relatively low molecular weight (e.g. <1 kDa) (Lewis et al. 1991). Although antibiotics with broad spectra of activity against many fungi and bacteria (e.g. tropolone) may eliminate or reduce beneficial microorganisms, most antibiotics are more selective in activity against pathogens (O'Sullivan & O'Gara 1992). Whipps (1997a) and Thomashow (1988) indicated that some suppression may be related to antibiotic or siderophore production, but stressed that further research is required in this area.

Antibiotic production by fluorescent pseudomonads has been implicated as an important mechanism mediating pathogen suppression (Wong & Baker 1984; Thomashow & Weller 1988; Shanahan et al. 1992; You & Sivasithamparam 1994). Production of antimicrobial compounds, including nitrogen-containing heterocycles: phenazines, pyrrol-type derivatives (pyrrolnitrin), pyo-compounds (pyocyanin, pyoluteorin), indole derivatives, and non-nitrogen-containing compounds (a minor class) including 2,4-diacetylphloroglucinol (DAPG), by some strains of Pseudomonas has been recognized as an effective mechanism of action for suppression of root pathogens (Dowling et al. 1996; O'Sullivan & O'Gara 1992; Shanahan et al. 1992). Garrett (1965) suggested that surfaces of fungal spores can stimulate growth of bacteria and actinomycetes which may then produce fungistatic substances sufficient to inhibit fungal spore germination. Bacillus species and their antibiotics isolated from composts are known to have antifungal activity against phytopathogenic fungi (Phae et al. 1990; Walker et al. 1998).

Lytic and other extracellular enzymes

Lytic and other extracellular enzymes may be produced by a variety of microorganisms to decrease competition for nutrients, space and other factors, by reducing numbers of other microorganisms. Lysis, or heterolysis, is a common mechanism of parasitism used by bacterial, fungal and other organisms on host tissues (Whipps 1997a). Many species of soil microorganisms produce enzymes (e.g. chitinase, glucanases) that hydrolyse major constituents of fungal cell walls (Ko & Lockwood 1970). Soil conditions that may cause lysis include high moisture content and increased bacterial numbers (Lockwood & Filonow 1981). Lytic enzymes such as chitinases, proteases, amylases or glucanases produced by actinomycetes and some bacterial and fungal species can result in the degradation of the structural matrix of fungal cell walls (Oppenheim & Chet 1992; Lorito et al. 1994). Because fungal cell walls contain chitin, the control of soil-borne fungal plant pathogens has been attempted through the addition of chitin to soil in efforts to increase chitin-decomposing microorganisms (Lockwood & Filonow 1981).

Although there have been comparatively fewer studies on bacterial enzyme production, it has been implicated as a significant factor in suppression of plant pathogens (Dunne *et al.* 1997; Berg *et al.* 1996; Dunne *et al.* 1998; Nelson 1991).

Parasitism and predation

Another proposed biological control strategy involves the use of mycoparasites to reduce the concentration of inoculum of a pathogen by enhancing degradation of dormant propagules, interfering with their formation, or inhibiting their germination (Fokkema 1993; Zhou & Boland 1997). Several mycoparasites and fungal antagonists are known to control pathogens by penetrating cell walls and other pathogen structures through a combination of physical pressure and enzymatic actions (Hadar & Gorodecki 1991; Geremia *et al.* 1993; Whipps *et al.* 1993; Lo *et al.* 1996; Zhou & Boland 1997; Hoitink *et al.* 1997b).

Studies to date have successfully used hypovirulent isolates of the turfgrass pathogen *Sclerotinia homoeocarpa* containing double-stranded RNA to reduce virulence in populations of this pathogen and improve disease management (Zhou & Boland 1995; Zhou & Boland 1998). Brown patch, caused by *Rhizoctonia solani* was suppressed through cross protection or induced resistance with non-pathogenic isolates of *Rhizoctonia* spp. in creeping bentgrass (Burpee & Goulty 1984). It was postulated that some isolates may have been hyperparasitic, but suppression was likely to be due to nutrient competition and/or host-induced resistance.

Host-mediated induction of resistance in plants

Host-mediated induction of resistance is a mechanism of biological control whereby resistance may be induced in plants, locally and systemically (Lucas 1998). Through colonization of various plant structures, many biocontrol agents exhibit a range of direct and indirect mechanisms that may prevent or delay infection in the host by pathogens (Whipps 1997a). Also termed systemic acquired resistance (SAR), this type of pathogen resistance in plants can be induced by chemicals, pathogens and beneficial soil microorganisms (Zhang et al. 1998). Microbe-induced elevated enzyme activity in plants results in improved defence against disease (Hoitink et al. 1997b). Host-mediated biological control may be induced through modification of the soil environment where microorganism populations may be shifted in a desired direction by making appropriate changes in soil conditions (Garrett 1965). This is commonly accomplished through application of organic amendments, such as green manures, crop residues (Garrett 1965), and composted materials (Hoitink & Fahy 1986). When applied to a plant system, microbes present in composts may promote plant growth or induce plants (e.g. hosts) to produce certain enzymes related to defense mechanisms (Arshad & Frankenberger 1991; Lucas 1998). Inhibition of disease through cross protection or induced resistance is another method of biocontrol, resulting from the prior or simultaneous inoculation of the host with a close avirulent relative of the pathogen (e.g. the same genus and/or species) (Cook & Baker 1983; Lucas 1998). This type of resistance is generally involved with expression of a set of genes within the plant, including those which encode for pathogenesis-related proteins such as chitinases, β -1,3-glucanases and thymidine-like proteins with antifungal properties (Linthorst 1991; Ward et al. 1991).

Conclusions

The classical biological control concept of the use of specific antagonists (inoculation) to control pathogens is being replaced by an alternative practice involving the introduction of functional antagonistic microbial communities in the form of soil amendments, especially composts. The variability currently seen among different composts for control of turfgrass diseases indicates that further research is needed to create uniform standards and performance levels (Block 1997). When variability in the product is lowered to acceptable levels, compost may be a product that provides effective suppression of turfgrass diseases, contributing to subsequent reduction in fungicide use. Problems with the use of soil amendments are a result of inadequate understanding of microbial ecology, and aspects leading to sustained performance of biocontrol agents (Lucas 1998). A key feature of effective suppression is the ability of microorganism populations to persist in soil and aggressively colonize the rhizosphere. An improved understanding of microbial community function will lead to the development of more effective, integrated strategies for the control of pathogens. Although it may be unreasonable to expect that natural agents will be a complete substitute for chemicals, the use of materials such as compost, will not only suppress disease but, more importantly, will slow the development of fungicide resistance in pathogens by permitting a reduction in the amount and frequency of use of chemical controls.

The general lack of interest in research on biological controls for turfgrass diseases in the past has resulted in many potential antagonists still in the development stage and/or recently marketed agents with unknown/unidentified mechanisms of control. The recently established ability for compost to act as a suppressive agent has led to continually increasing research surrounding the development of consistency in control and increased knowledge – or, at least awareness of – the large number of factors in composts which play an integrated role in pathogen suppression.

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