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Soil binding properties of mucilage produced by a basidiomycete fungus in a model system

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A saprophytic, lignin-decomposing basidiomycete fungal isolate (BB1), identified as a member of the russuloid lineage closest to the genus *Peniophora*, plays a role in soil aggregation and stabilization. In liquid media this fungus secretes large amounts of extracellular materials or mucilage that act as soil binding agents. We investigated the nature of these materials using periodate treatment and lectin cytochemistry, and studied whether or not these materials are involved in soil aggregation. Water stability of artificial fungal amended soil aggregates was destroyed by periodate treatment suggesting that polysaccharides produced by the basidiomycete were involved in soil aggregation. Binding patterns of fluorescently labeled lectins were also investigated to determine specific carbohydrate moieties present in the fungal mucilage. Fluorescently conjugated lectins (*Ulex europaeus* Agglutinin I and *Lotus tetragonolobus* lectin) bound to extracellular mucilage indicating that this basidiomycete mucilage contains fucosyl sugar residues. We also demonstrated that water stability of artificial soil aggregates prepared with fungal mycelia pretreated with L(−)fucose lectins were significantly reduced. This study indicates that fungal-derived material containing fucosyl residues plays a role in soil adhesion.

INTRODUCTION

Tisdall & Oades (1982) proposed a hierarchical model of soil aggregation processes in which clay particles are bound together into persistent microaggregates (2–20 μm diam) by inorganic binding agents consisting of amorphous aluminosilicates, oxides, humic substances, and soil polysaccharides associated with di- or trivalent metal ions. These microaggregates may be bound together with plant debris into larger microaggregates (20–250 μm diam) by temporary binding agents consisting of roots, root hairs, and fungal hyphae. The microaggregates in turn are bound into macroaggregates (> 250 μm diam) which are maintained by transient binding agents in soil including readily decomposable organic materials from plant and microbial origin, the most important of which are polysaccharides and polyuronides.

Most of the extracellular materials present on the surface of the fungal cell are carbohydrate containing molecules. Analysis of fungal cell wall extracts demonstrated that outer layers contain a complex array of (glyco) proteins (Aronson 1965), polysaccharides (Barnicki-Garcia 1968, Rosenberger 1976), lipids (lipoproteins) (Weete 1980), and pigments (Arpin & Fiasson 1971). Although the mechanism of their synthesis and deposition is still poorly understood, it is well recognized that extracellular polysaccharides produced by microbes can have several functions. Besides roles in adhesion (Nicholson 1984), protection against desiccation, freezing, water potential fluctuations (Rudolph & Crowe 1985), and as a buffer between cells and toxic environments (Gadd 1986), these polysaccharides aggregate soil particles (Mehta *et al.* 1960, Clapp *et al.* 1962, Martin 1971, Griffiths & Burns 1972, Chenu 1989, Wright & Upadhyaya 1996). The evidence for the role of extracellular polysaccharides produced by fungi in soil aggregation is based on the aggregating action of extracted fungal polysaccharides. Chenu (1989) demonstrated that scleroglucan, a capsular polysaccharide produced by species of *Sclerotium*, can increase the stability of both kaolinitic and montmorillonitic clays forming organo-mineral networks. Wright & Upadhyaya (1996) extracted glycoproteinaceous substances named glomalin from soil aggregates.

The fungus isolate (BB1) used in this study was identified as a member of the russuloid clade of *Homobasidiomycetes* (Hibbett *et al.* 1997, Hibbett & Thorn 2001). Phylogenetic analyses of BB1 rDNA identified this

[1] *Abbreviations*: Con A, Concanavalin A; DBA, *Dolochos biflorus* agglutinin; FITC, Fluorescein isothiocyanate; LTL, *Lotus tetragonolobus* lectin; PNA, peanut agglutinin; PBS, phosphate buffer saline; UEA I, *Ulex europaeus* agglutinin I; RCA_{120}, *Ricinus communis* agglutinin I; WGA, wheat germ agglutinin.

isolate as a member of russuloid lineage, closest to the genus *Peniophora* (Caesar-TonThat *et al*. 2001). *Peniophora* is a genus of lignocellulose degrading white rot with crust-like fruiting bodies that form on the undersides of dead logs, branches, twigs, and plant residues (Ginns & Lefevre 1993). Species of *Peniophora* are mostly found in forest and they not known to occur in soil, but do fruit on plant debris in contact with soil (Ginns & Lefevre 1993). Isolate BB1 was from surface plant debris agricultural soil and was shown to produce large amounts of water-insoluble mucilage that efficiently bind sandy soil particles (Caesar-TonThat & Cochran 2000). This isolate also secrete ligninolytic enzymes demonstrated in culture medium containing guaiacol as a substrate (Caesar-TonThat & Cochran 2000). Nothing is known about the role of lignin-degrading basidiomycete fungi in cropland, however their presence in agricultural soils is not surprising because small grains known to contain high amount of lignin, are common agricultural crops in eastern Montana. For example, barley contains 10–12 g lignin 100 g of stems^{-1} (Cochran 1991). Moreover, management practices such as conservation tillage and no till have become more popular in the Northern Great Plains, resulting in surface accumulation of crop plant residues. In this study, a periodate treatment method developed by Cheshire, Sparling & Mundie (1983) was used to investigate the carbohydrate nature of the mucilage secreted by BB1 and the implications of these materials in soil aggregation.

In view of the presumptive evidence that polysaccharides secreted by the basidiomycete play a role in soil aggregation, it was desirable to analyze the sugar residues present in the carbohydrates and examine their role in aggregating soil particles. The estimation of surface carbohydrates using traditional biochemical methods has a number of technical problems, since chemical treatment of hyphae is not restricted to their surfaces. Functional entities may be degraded and such methods are not selective enough (Wessels & Sietsma 1981). Therefore, plant lectins, non-enzymatic proteins with high affinities for mono- and oligosaccharides were utilized to label specific residues on the fungal surface (Erdos 1986). This method has been used successfully with a number of phytopathogenic fungi (Pistole 1981).

As a preliminary step in identifying cell surface receptors for soil binding, this paper reports that of a battery of lectins tested, only those binding to fucosyl residues bound to the cell surface of BB1.

MATERIALS AND METHODS

Fungal cultures

Fungal isolation was previously described (Caesar-TonThat & Cochran 2000). The fungus was cultured in potato dextrose broth (Difco Laboratories, Detroit, MI) for 4 weeks at room temperature on a shaker set at 150 rpm.

Preparation of artificial fungal-amended aggregates

Artificial fungal-amended aggregates were prepared as described previously (Caesar-TonThat & Cochran 2000). Briefly, air-dried soil (14% clay, 14% silt, and 72% sand) was passed through a 0.25 mm sieve to remove large soil particles before mixing with 4-week-old homogenized mycelia (0.3 g g^{-1} soil). The soil mixture was uniformly wetted with distilled water and air dried in a forced-air oven for 24 h at 60 °C. The resulting soil cake was manually ground with a pestle into particles of approx. 1–2 mm.

Sodium periodate treatment

The effects of periodate oxidation on artificial fungal amended soil aggregates were tested according to a method modified from Cheshire *et al*. (1983). These authors showed that oxidation of soil with periodate increased the disruption of soil aggregates and that the degree of disruption was highly correlated with the residual level of reducing sugars (after hydrolysis). To test the effects of periodate oxidation on fungal-amended soil aggregates, 5 g samples were added to glass beakers (100 ml volume) and immersed in 20 ml of sodium chloride solution (NaCl, 0.05 M) for 24 h at 22 °. Treatment with sodium chloride permits rapid diffusion of periodate ions into the soil aggregates (Clapp & Emerson 1965b). Soil aggregates were allowed to sediment and the sodium chloride solution was replaced by 20 ml of sodium periodate ($NaIO_4$, 0.05 M) (Sigma, St Louis, MO). Fungal-amended aggregates were incubated for a total period of 12 h in the sodium periodate solution and they were gently agitated by hand every 15 min. Replicate aliquots were removed at 1 h intervals. The sodium periodate solution was decanted, replaced by 20 ml of sodium tetraborate ($Na_2B_4O_7$, 0.1 M, pH 9.6; Sigma), and incubated for an additional 2 h. Samples were then passed through a 0.25 mm sieve. The soil aggregate fractions collected on the sieve were oven-dried at 60 ° for 24 h and weighed. Controls were treated with sodium chloride then with distilled water or only with distilled water.

Treatment on fungal mycelia with sodium periodate was intended to demonstrate whether or not extracellular fungal materials contain polysaccharides and polyuronides that are responsible for soil aggregation. Samples of 5 g of mycelia (wet weight) were treated aseptically and under continuous agitation (100 rpm) with sodium periodate for a total incubation period of 6 h. A concentration of 0.025 M $NaIO_4$, was used to treat fungal mycelia instead of 0.05 M used to treat fungal-amended soil aggregates. Replicate aliquots were removed at 1 h intervals. The sodium periodate solution was replaced by sodium tetraborate solution ($Na_2B_4O_7$, 0.1 M, pH 9.6) and mycelia were incubated for an additional 2 h. After treatment, mycelia were washed with distilled water through filtration using Whatman paper No. 1, homogenized (Brinkmann Instruments, Westbury, NY) for 30 s, then mixed with soil to generate

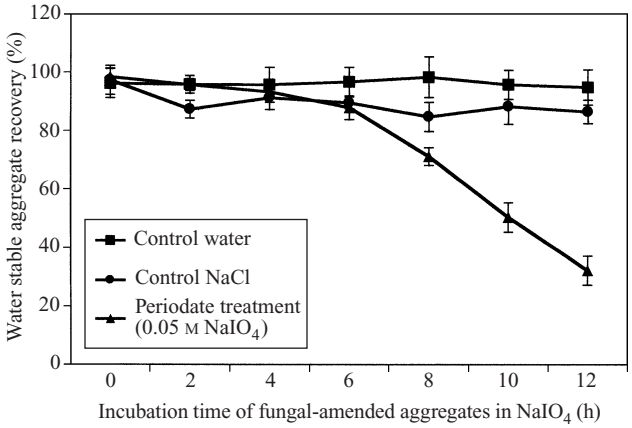


Fig. 1. Effects of periodate treatment on artificial aggregates. Change with time in water stability of fungal-amended aggregates after treatment with: (▲) 0.05 M NaCl and 0.05 M $NaIO_4$ followed by 0.1 M $Na_2B_4O_7$ at pH 9.6; (■) distilled water; (●) 0.05 M NaCl. Bars indicate standard errors of the mean of three replicates.

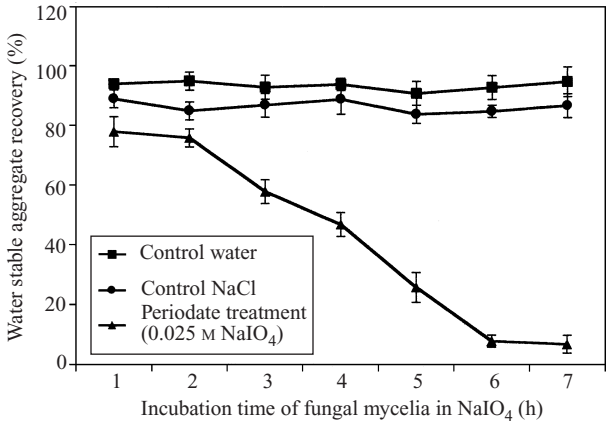


Fig. 2. Change in water stability of soil aggregates prepared with fungal mycelia treated with sodium periodate. (▲) 0.05 M NaCl and 0.025 M $NaIO_4$ followed by 0.1 M $Na_2B_4O_7$ at pH 9.6; (■) distilled water; (●) 0.05 M NaCl. Bars indicate standard errors of the mean of three replicates.

artificial aggregates. The mixture was oven-dried at 60 °. The dried soil cake was broken into 1–2 mm aggregates and water stability was determined by a modification according to the procedure of Kemper & Rosenau (1986). The percentage of water stable aggregate was defined as the portion of the original sample that remained on the sieve. Each determination was made in triplicate.

Staining with lectins

A set of samples of fungal mycelia were mixed for 1 h in 3% formaldehyde in 0.1 M sodium phosphate buffer (PBS), pH 7.4. To prevent free aldehydes from non-specifically crosslinking with lectins, mycelia were washed twice with the same buffer, which included 0.05 M glycine (Gilboa-Garber & Mizrahi 1980) and an additional 2 times with PBS before treatment with lectin compounds. FITC-labeled lectins were obtained from Vector Laboratories (Burlingame, CA, USA) and represent a range of carbohydrate-binding capabilities. The following lectins were used in the present experiments to determine the respective carbohydrates: Con A for α-mannose; WGA for β-1,4-*N*-acetylglucosamine, SBA for α- and β-*N*-acetylgalactosamine, UEA I and LTL for α-L-fucose, RCA_{120} for oligosaccharides ending in galactose, PNA for β-1,3-*N*-acetylgalactosamine and α and β-galactose, DBA for α-*N*-acetylgalactosamine. All lectins were dissolved in PBS at a final concentration of 20 μg ml^{-1}. Formaldehyde-fixed mycelia were incubated in lectin solutions for 10 min to 1 h at room temperature. They were then washed in PBS and distilled water and mounted on anti-fade medium of 1,4-diazabicyclo [2,2,2]octaine (Sigma) and 2.5 mg ml^{-1} Glycergel (Dako Corporation, Carpinteria, CA) before viewing. Inhibition by specific hapten sugars was performed to verify specificity of lectin binding. For hapten binding controls, the lectins were bound with their specific sugar. Haptens used were L(−)fucose for UEA I or LTL, α-methyl mannoside for ConA, *N*,*N*′,*N*″-triacetyl-chitotriose for WGA, *N*-acetyl-D-galactosamine for SBA, galactose for RCA_{120} or PNA, and *N*-acetyl-galactosamine for DBA (Sigma). To prepare controls, 200 mM of hapten inhibitor was incubated with the lectin solution before it was added to the cells. Material was examined with a Zeiss Axiovert S 100 TV equipped with fluorescent optics. The microscope was fitted with a HBO 50 W lamp and FITC filter set with exciter filter transmitting at 450–490 nm and barrier filter transmitting above 520 nm. Photographs were taken on Kodak T Max film rated at 1600 ASA.

To determine whether or not UEA I, LTL, WGA, and ConA can alter the surface mucilage and reduce the capacity of fungal mycelia to aggregate soil particles, mycelia were pretreated for 2 h at 20 ° with non-conjugated lectins at 0.01, 0.2, and 0.4 mg ml^{-1} in PBS. Mycelia were washed 3 times for 5 min with PBS then they were mixed with soil to form artificial aggregates as described above. Aggregates produced with lectin-treated mycelia were tested for their water stability using the wet sieving analysis as described previously (Caesar-TonThat & Cochran 2000). In the controls, mycelia were treated with lectins that were previously incubated for 30 min with their respective hapten sugars before mixing with soil to form aggregates. The experiments were repeated three times. The data were analyzed statistically using ANOVA. These analyses were accomplished using Stat View (SAS Institute) (Abacus Concepts 1987).

Low temperature scanning electron microscopy

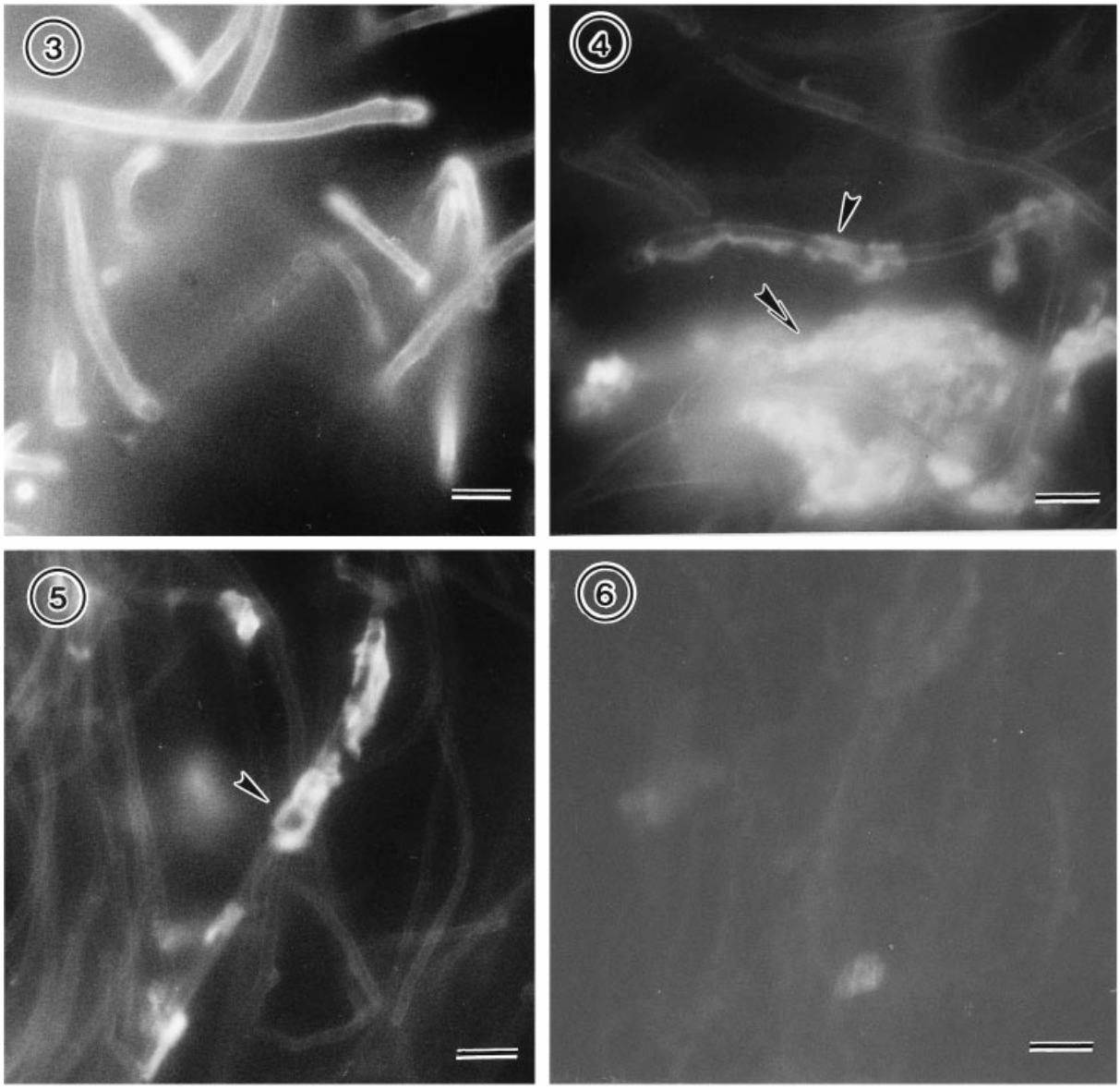
Small pieces of mycelia were deposited on an aluminum stub on a thin layer of embedding medium (Tissue-Tek, Torrance, CA). The materials were plunged into nitrogen slush ($\leqslant -210$ °), then the frozen-hydrated tissue was transferred under vacuum to a cryopreparation unit (Oxford CT 1500) attached to a scanning electron microscope (SEM) JEOL JSM-6100 equipped

with a LaB6 source and turbomolecular pumping. The materials were gold sputter coated to a thickness of approx. 1–2 nm inside the cryopreparation chamber and transferred to the main chamber of the SEM to be analyzed. During sample analysis, the pressure in the SEM chamber was 1×10^6 Torr and the acceleration voltage set at 12 kV.

RESULTS

When soil aggregates artificially prepared with mycelia from the basidiomycete fungal isolate BB1 were treated with sodium periodate, more than 87.83% of soil aggregates remained water stable after 6 h treatment and only 32.17% of aggregates remained water stable after 12 h (Fig. 1). Thereafter, the amount of water stable aggregates decreased steadily. Aggregates incubated in water and in 0.05 M NaCl retained their water stability.

When mycelia were treated with sodium periodate (0.025 M $NaIO_4$) for 1 h then mixed with soil to generate artificial soil aggregates, 78% of the soil aggregates remained water stable (Fig. 2). Only 8.2% of soil aggregates made with mycelia previously treated with sodium periodate for 6 h were water stable. In control samples, soil aggregates prepared with mycelia treated



Figs 3–6. Staining of fungal mycelia from basidiomycete isolate BB1 with lectins. **Fig. 3.** Staining with FITC-WGA. Mycelia bind intensively FITC-WGA resulting in strong fluorescence at the cell wall. **Fig. 4.** Staining with FITC-UEA I. Low fluorescence is detected along the mycelial cell wall. Intense fluorescence is found on mucilage still attached (single arrow) to or sloughed off (double arrow) from the cell surface. **Fig. 5.** Staining with FITC-LTL. Fluorescence is detected on mucilage attached to the mycelial cell wall (arrow). Mycelial cell wall is slightly stained. **Fig. 6.** Staining of fungal mycelia with FITC-UEA I after sodium periodate treatment followed by sodium tetraborate for 6 h. No fluorescence staining is detected. Bars = 5 μm.

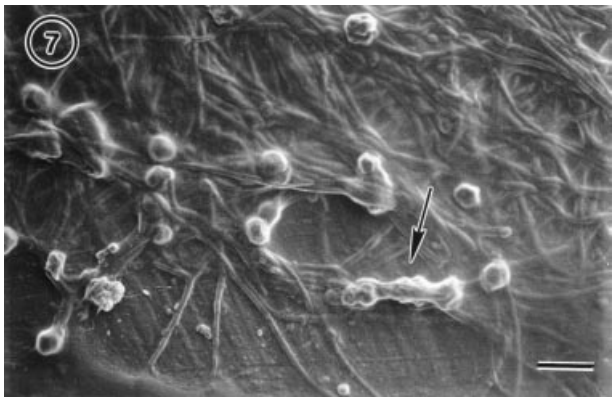


Fig. 7. Low temperature scanning electron micrograph of 4-week-old mycelium showing accumulation of extracellular mucilaginous materials (arrow). Bar = 20 μm.

water or 0.05 M NaCl treated mycelia retained their water stability.

Fixation with 3% formaldehyde did not induce fluorescence. Consequently, all staining was made with formaldehyde fixed materials. Among the FITC-conjugated lectins used in this study to stain fungal mycelia, only staining with FITC-WGA, FITC-UEA I and FITC-LTL resulted in detectable fluorescence (Figs 3–5). The binding pattern of FITC-WGA differed from FITC-UEA I and FITC-LTL. FITC-WGA bound extensively over the mycelial surface and also throughout the cytoplasm, with distinct areas of bright and low fluorescence (Fig. 3). Unlike FITC-WGA, the fluorescent staining with FITC-UEA I (Fig. 4) and FITC-LTL (Fig. 5) was only weakly visible along the cell surface of hyphal cells. However, patches of intense fluorescence were observed randomly in the mycelial preparation. These fluorescent regions presented different shapes, ranging from discrete patches on the cell surface (Figs 4–5, single arrow) to large globules (Fig. 4, double arrow). Mycelia treated with sodium periodate for 6 h showed no fluorescence after staining with FITC-UEA (Fig. 6). Because these fluorescent extracellular materials produced by the mycelia were not visible under the bright field or phase contrast optics, scanning electron microscopy was utilized to demonstrate whether or not they could be correlated to some morphological structures. Using low temperature scanning electron microscopy, mycelia showed extracellular materials that were spatially distributed the same way as the materials that fluoresce after FITC-UEA or FITC-LTL staining (Fig. 7). There was no binding of FITC-ConA, FITC-SBA, FITC-RCA_{120}, FITC-PNA, and FITC-DBA on fungal mycelia. No fluorescence was detected with either FITC-UEAI or FITC-LTL when the lectin was pre-incubated with fucose.

Water stability was compared between artificial soil aggregates amended with fungal mycelia previously treated for 2 h with non-conjugated lectins (UEA I, LTL, WGA and Con A) at 0.01, 0.2 and 0.4 mg ml^{-1} and the control aggregates amended with water fungal mycelia (Table 1). Significant reduction in water stable aggregate recovery was found in aggregates amended with fungal mycelia pretreated with the L(−)fucose lectins (UEA I and LTL) at 0.2 and 0.4 mg ml^{-1}. Aggregates amended with WGA- and ConA-pretreated mycelia did not result in loss of water aggregate stability. No significant change was found in stability of aggregates prepared with mycelia pretreated with lectins in presence of their appropriate hapten sugars.

Table 1. Effects of modifications of fungal cell surface with lectins on water stability of artificial fungal-amended aggregates.

Pretreatment	Water stable aggregate recovery (%)
Water†	98.06 ± 8.53
Ulex europaeus lectin I (UEA I)	[a]93.08 ± 10.74 [b]80.74 ± 8.64* [c]75.99 ± 14.70**
UEA I + 0.05 M L(−)fucose	[c]98.45 ± 6.95
Lotus tetragonobolus lectin (LTL)	[a]89.47 ± 10.90 [b]82.39 ± 9.65* [c]71.75 ± 2.27**
LTL + 0.05 M L(−)fucose	[c]95.5 ± 4.43
Wheat germ agglutinin (WGA)	[a]91.63 ± 8.98 [b]98.31 ± 7.63 [c]96.08 ± 2.66
WGA + 0.02 mM methyl-2-acetomido-2-deoxy-β-D-glucopyranoside	[c]98.06 ± 3.21
Concanavalin A (ConA)	[a]97.72 ± 9.35 [b]93.47 ± 11.43 [c]98.61 ± 7.53
ConA + 0.02 mM methyl α-mannoside	[c]97.34 ± 1.86

† Water is the control for all treatments since pretreatment with the buffer used to prepare lectins (PBS) did not significantly affect aggregation of soil particles. Significantly different from control in water: $*P < 0.01$; $**P < 0.001$.

Lectin concentration at [a] 0.01 mg ml^{-1}; [b] 0.2 ml ml^{-1}; [c] 0.4 mg ml^{-1}.

DISCUSSION

The most important property associated with soil polysaccharides is the binding of soil particles into water stable aggregates. Several studies on binding action of soil polysaccharides of humus origin (Mehta *et al.* 1960, Martin 1971) or from microbial origin in general (Griffiths 1965, Griffiths & Burns 1972, Chenu 1989, Molope, Grieve & Page 1987, Robertson, Sarig & Firestone 1991) have been published. However, so far no work has been reported concerning soil binding of polysaccharides from a specific fungal species. Results of this present study provide further information on soil aggregation by a saprophytic, lignin decomposing russuloid basidiomycete fungus.

Periodate followed by sodium tetraborate treatment destroys long-chain polysaccharides, thus disrupting soil aggregates. This treatment has been used to demon-

strate the presence of carbohydrates in natural soil aggregates (Mehta *et al.* 1960, Greenland, Lindstrom & Quirk 1962, Clapp & Emerson 1965a, b, Cheshire *et al.* 1983, 1984, Sparling & Cheshire 1985, Stefanson 1971, Molope *et al.* 1987). Periodate oxidizes the glycol groups of the sugar units of the polysaccharides and polyuronides (Bobbit 1956). The oxidized polymers are partially degraded in alkaline solution (Whistler & BeMiller 1958). Sodium tetraborate treatment is used to complete the degradation of these polymers. We demonstrated that the formation of water stable soil aggregates by the russuloid fungal isolate BB1 is sensitive to periodate treatment indicating the involvement of extracellular basidiomycete-derived polysaccharides in soil aggregation. A 6 h chemical treatment on fungal-amended aggregates was required to induce disruption of the aggregates in water, whereas it needed only 2 h to treat fungal mycelia with sodium periodate for the aggregates to loose their water stability. Because periodate treatment was processed on dry artificial fungal-amended aggregates, air-drying of the aggregates may tighten bridge linkages between polysaccharides and clay in soil as suggested by many authors (Greenland 1956, Emerson, Foster & Oades 1986), leading to more resistance of the polysaccharides to periodate treatment. When fungal mycelia was treated with periodate before preparation of aggregates, most polysaccharides attached to the cell surface may have been destroyed, resulting in less ability to form resistant bonds during drying.

Fungi are known to secrete polysaccharides with 'adhesive' qualities, which can adsorb soil clay particles (Foster 1981, Chenu 1989) but relatively little is known about the mechanisms by which clays adhere to fungal mycelium. The cell wall of most septate fungi is composed of four intergrading regions: (1) an outermost cell wall layer (80–90 nm thick) of amorphous glucans containing β-1,3 and β-1,6 linkages, (2) a glycoprotein network (40–50 nm thick), in which the glucans merge into the protein layer; (3) a discrete protein layer; and (4) an innermost layer (20 nm thick) of chitin microfibrils (Bartnicki-Garcia 1968, Burnett 1976, Fleet & Phaff 1981). Since fungal mycelium has a net negative charge, it is likely to attract the positively charged edge of clay particles in soil and bring about soil aggregation. The occurrence of hydrogen bonding between the β-glucan on the outer surface of the fungal cell wall and waters of hydration on the soil clay particle has been suggested as a mechanism of fungal soil clay adsorption (Lavie & Stotsky 1986).

Using lectins to label specific sugar residues on fungal surfaces (Benhamou 1988, Erdos 1986), we demonstrated that the mucilage secreted by the basidiomycete fungus contains fucosyl sugar residues after staining with FITC conjugated L(−)fucose binding lectins. Fluorescence of fucosyl sugar residues was detected on materials attached to (Figs 4–5, single arrow) or sloughed off from the fungal cell wall (Fig. 4, double arrows). In contrast to the intense fluorescence of the cell wall observed after staining with FITC-WGA indicating the presence of *N*-acetylglucosamine residues, there was low fluorescence seen on the cell wall stained with FITC conjugated L(−)fucose lectins. L(−)fucose lectins used in this study were similar in their binding properties; like LTL, UEA I interacts with 6-*O*-alpha-L-fucosyl-*N*-acetylglucosamine and its related asparagine-linked glycopeptide, but is unable to bind to internal alpha-L-fucosyl units (Goldstein & Poretz 1986). Deoxyhexoses, including L-fucose (6-deoxygalactose) and L-rhamnose, are known to exist in microorganisms (Finch, Hayes & Stacey 1971, Greenland & Oades 1975, Cheshire 1979). In fungi, heteropolysaccharides containing fucose have been isolated from basidiomycetes belonging to the *Polyporaceae* (Bhavanandan, Bouveng & Lindberg 1964, Fraser, Karaesoni & Lindberg 1967, Bjorndal & Wagstrom 1969). Fucose was also found in the extracellular materials produced by a white rot basidiomycete *Phlebia radiata* (Krcmar *et al.* 1999). Polysaccharide fractions isolated from *Mucorales* species were reported to contain glucuronic acids and fucose (Bartnicki-Garcia & Reyes 1968, Tsuchihashi, Yadomae & Miyazaki 1983). Fucose moieties were also found in germ tube tip mucilage of the fungal rice blast pathogen *Magnaporthe grisea* (T. M. Bourett & R. J. Howard, pers. comm.). In bacteria, rhamnose and fucose were found in the cell membrane of *Azospirillum brasilense* mucopolysaccharides and polysaccharides (Skvortsov & Ignatov 1998). Although fucose was reported to be present in plant root mucilage and to have adhesion properties (Hinch & Clarke 1980, Vermeer & McCully 1981, Watt *et al.* 1993), the function of fucosyl residues in microorganisms is not well known. Several species of the yeast *Candida albicans* were shown to contain on their cell wall surface fucosyl and *N*-acetylglucosaminyl-containing residues that were demonstrated to play a role in the adhesion process to exfoliated buccal epithelial cells (Critchley & Douglas 1987).

We demonstrated that soil aggregation ability of the fungus significantly decreased when fucosyl residues sites were not available for binding soil particles. These results indicate that these sugar residues produced by the basidiomycete fungus and present in the extracellular mucilage exhibit adhesion properties. The ability of soil particles to aggregate to each other could also depend on the integrity of the fungal cell surface components of this basidiomycete fungus. Understanding surface interactions between fungi and soil particulates could provide valuable information for the development of agricultural management techniques that have potential to increase populations of basidiomycete fungi with ability to aggregate soil.

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