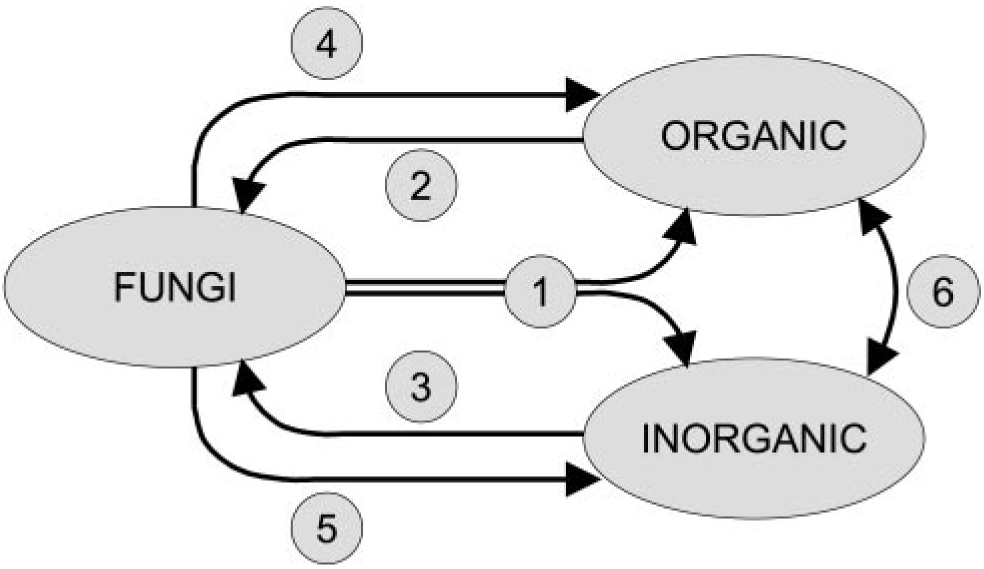
Table 2. Roles and activities of fungi in biogeochemical processes (slightly modified from Table 1 in Gadd, 2007).	
Fungal role and/or activity	**Biogeochemical consequences**
Growth and mycelium development	Stabilization of soil structure; soil particulate aggregation; penetration of pores, fissures, and grain boundaries in rocks and minerals; mineral tunnelling; biomechanical disruption of solid substrates; plant colonization and/or infection (mycorrhizas, pathogens, parasites); animal colonization and/or infection (symbiotic, pathogens, parasites); translocation of inorganic and organic nutrients; assisted redistribution of bacteria; production of exopolymeric substances (serve as nutrient resource for other organisms); water retention and translocation; surfaces for bacterial growth, transport and migration; cord formation (enhanced nutrient translocation); mycelium acting as a reservoir of nitrogen and/or other elements (e.g. wood decay fungi).
Metabolism: Carbon and energy metabolism	Organic matter decomposition; cycling and/or transformations of component elements of organic compounds and biomass: carbon, hydrogen, oxygen, nitrogen, phosphorus, sulphur, metals, metalloids, radionuclides (natural and accumulated from anthropogenic sources); breakdown of polymers; altered geochemistry of local environment, e.g. changes in redox, oxygen, pH; production of inorganic and organic metabolites, e.g. protons, carbon dioxide, organic acids, with resultant effects on the substrate; extracellular enzyme production; fossil fuel degradation; oxalate formation; metalloid methylation (e.g. arsenic, selenium); xenobiotic degradation (e.g. polynuclear aromatic hydrocarbons); organometal formation and/or degradation (note: lack of fungal decomposition in anaerobic conditions caused by water logging can lead to organic soil formation, e.g. peat).
Inorganic nutrition	Altered distribution and cycling of inorganic nutrient species, e.g. nitrogen, sulphur, phosphorus, essential and inessential metals, by transport and accumulation; transformation and incorporation of inorganic elements into macromolecules; alterations in oxidation state; metal(loid) oxido-reductions; heterotrophic nitrification; siderophore production for iron(III) capture; translocation of nitrogen, phosphorus, calcium, magnesium, sodium, potassium through mycelium and/or to plant hosts; water transport to and from plant hosts; metalloid oxyanion transport and accumulation; degradation of organic and inorganic sulphur compounds.
Mineral dissolution	Rock and mineral deterioration and bioweathering including carbonates, silicates, phosphates and sulphides; bioleaching of metals and other components; manganese dioxide (MnO2) reduction; element redistributions including transfer from terrestrial to aquatic systems; altered bioavailability of, e.g. metals, phosphorus, sulphur, silicon, aluminium; altered plant and microbial nutrition or toxicity; early stages of mineral soil formation; deterioration of building stone, cement, plaster, concrete etc.
Mineral formation	Element immobilization including metals, radionuclides, carbon, phosphorus, and sulphur; mycogenic carbonate formation; limestone calcrete cementation; mycogenic metal oxalate formation; metal detoxification; contribution to patinas on rocks (e.g. 'desert varnish'); soil storage of carbon and other elements.
Physico-chemical properties. Sorption of soluble and particulate metal species. Exopolysaccharide production	Altered metal distribution and bioavailability; metal detoxification; metal-loaded food source for invertebrates; prelude to secondary mineral formation. Complexation of cations; provision of hydrated matrix for mineral formation; enhanced adherence to substrate; clay mineral binding; stabilization of soil aggregates; matrix for bacterial growth; chemical interactions of exopolysaccharide with mineral substrates.

Mutualistic symbiotic associations: mycorrhizas, lichens, insects and other invertebrates.	Altered mobility and bioavailability of nutrient and inessential metals, nitrogen, phosphorus, sulphur, etc; altered carbon flow and transfer between plant, fungus and rhizosphere organisms; altered plant productivity; mineral dissolution and metal and nutrient release from bound and mineral sources; altered biogeochemistry in soil–plant root region; altered microbial activity in plant root region; altered metal distributions between plant and fungus; water transport to and from the plant. Pioneer colonization of rocks and minerals; bioweathering; mineral dissolution and/or formation; metal accumulation and redistribution; metal accumulation by dry or wet deposition, particulate entrapment; metal sorption; enrichment of carbon, nitrogen, etc; early stages of mineral soil formation; development of geochemically-active microbial populations; mineral dissolution by metabolites including 'lichen acids'; biophysical disruption of substrate. Fungal populations in gut aid degradation of plant material; invertebrates mechanically render plant residues more amenable for decomposition; cultivation of fungal gardens by certain insects (organic matter decomposition and recycling); transfer of fungi between plant hosts by insects (aiding infection and disease).
Pathogenic effects: plant and animal pathogenicity	Plant infection and colonization; animal predation (e.g. nematodes) and infection (e.g. insects, etc); redistribution of elements and nutrients; increased supply of organic material for decomposition; stimulation of other geochemically-active microbial populations.

Such activities take place in aquatic and terrestrial ecosystems, as well as in artificial and man-made systems, their relative importance depending on the species present and physico-chemical factors that affect activity. The terrestrial environment is the main locale of fungal-mediated biogeochemical change, especially in mineral soils and the plant root zone, and on exposed rocks and mineral surfaces. There is rather a limited amount of knowledge on fungal biogeochemistry in freshwater and marine systems, sediments, and the deep subsurface. Fungal roles have been arbitrarily split into categories based on growth, organic and inorganic metabolism, physicochemical attributes, and symbiotic relationships. However, it should be noted that many if not all of these are inter-linked, and almost all directly or indirectly depend on the mode of fungal growth (including symbiotic relationships) and accompanying heterotrophic metabolism, in turn dependent on a utilizable carbon source for biosynthesis and energy, and other essential elements, such as nitrogen, oxygen, phosphorus, sulphur and many metals, for structural and cellular components. Mineral dissolution and formation are outlined separately although these processes clearly depend on metabolic activity and growth form (from Gadd 2007).



Diagrammatic representation of fungal action on organic and inorganic substrates which may be naturally-occurring and/or produced by man. **1**. organic and inorganic transformations mediated by enzymes and metabolites, e.g. H^+, CO_2, and organic acids, and physico-chemical changes occurring as a result of metabolism; **2**. uptake, metabolism or degradation of organic substrates; **3**. uptake, accumulation, sorption, metabolism of inorganic substrates; 4. production of organic metabolites, exopolymers, and biomass; **5**. production of inorganic metabolites, secondary minerals and transformed metal(loid)s; **6**. chemical interactions between organic and inorganic substances, e.g. complexation and chelation, which can modify bioavailability, toxicity and mobility. Translocation phenomena may also be associated with the organisms contributing to this model. From Gadd (2004).