

ADVANCES IN
Agronomy

VOLUME 106



ADVANCES IN AGRONOMY

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PREFACE

Volume 106 contains five outstanding reviews that focus on the impacts of climate change on the water cycle, crop production, and grassland fire management, phosphorus mobility and its effects on water quality, organic matter structure and interactions in the environment, and strategies for more effectively communicating soil science research findings. Chapter 1 discusses the role of drying and rewetting, and freezing and thawing on the mobilization of P to surface waters. Chapter 2 provides strategies for enhancing crop production in water-limited environments. Chapter 3 provides a contemporary and historical view of organic soil matter chemistry and its importance in the environment. Chapter 4 is a timely review on ways to enhance the dissemination of soil science research to the public and the policymakers. Chapter 5 covers the effects of climate change and increases in temperature on fire management of grasslands.

I am grateful to the authors for their fine reviews.

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PHOSPHORUS SOLUBILIZATION AND POTENTIAL TRANSFER TO SURFACE WATERS FROM THE SOIL MICROBIAL BIOMASS FOLLOWING DRYING–REWETTING AND FREEZING–THAWING

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Abstract

Drying–rewetting and freezing–thawing are two of the most common forms of abiotic perturbations experienced by soils, and can result in the solubilization of phosphorus (P). There is increasing interest in one particular component of soil P that may be especially susceptible to such stresses: the soil microbial biomass. We examine the evidence for the soil microbial biomass acting as a significant source of P in soils and surface waters by studying the literature on the processes responsible for its solubilization and transfer, resulting from abiotic perturbations. These perturbations have been shown to kill up to *circa* 70% of the total microbial biomass in some soils, and in some cases nearly all the additional P solubilized has been attributed to the microbial biomass. The degree to which the soil microbial biomass is affected by abiotic perturbations is highly dependent upon many variables, not the least degree, duration, and temporal patterns of stress, as well as the soil type. It is hypothesized that while abiotic perturbations can solubilize large quantities of P from the soil microbial biomass in some soils, only a small proportion is likely to find its way from the soil to surface waters. This is not to say that this small proportion is not significant with regard to surface water quality and nutrient loss from the soil, and may become more prevalent under future climatic change. We conclude that it is likely that only extreme conditions will elicit large responses with regard to the solubilization and transfer of phosphorus to surface waters.

1. INTRODUCTION

Soils experience a wide range of abiotic perturbations, including flooding, heating, freezing, drying, thawing, and compaction. However, drying–rewetting and freezing–thawing are two of the most common forms of abiotic perturbations (Soulides and Allison, 1961), and they play a critical role in soil nutrient dynamics and biogeochemistry. Both these perturbations are predicted to become more extreme with the United Nations Framework Convention on Climate Change (UNFCCC, 2008) stating that “. . . it is very likely that hot extremes, heat waves and heavy precipitation events will continue to become more frequent. . .” on a global scale, with many regions experiencing “. . . increased intensity of droughts and floods as a result of climate change.” These trends have potentially significant (but as yet not fully known) consequences for soil nutrient dynamics. The spatial extent of these perturbations is wide, with almost all soils experiencing moisture fluctuations to varying degrees and over different temporal periods due to wetting mechanisms, which include precipitation, riverine flooding, tidal flooding and irrigation. Soils that experience freezing and thawing are more limited in extent because they occur mostly at high altitudes and latitudes.

Despite this, approximately 55% of the total land area in the northern hemisphere experiences seasonally frozen ground (Zhang *et al.*, 2003).

Solubilization of nutrients in soils refers to the release of previously bound or fixed nutrients (such as those immobilized in the microbial biomass) into solution. Increases in nutrient solubilization within dried soils following their rewetting are widely reported particularly with regard to carbon (C) and nitrogen (N) (e.g., Denef *et al.*, 2001; Fierer and Schimel, 2002; Franzluebbers *et al.*, 1996; Gordon *et al.*, 2008; Mikha *et al.*, 2005; Van Gestel *et al.*, 1991; Venterink *et al.*, 2004), but less so for phosphorus (P) (Chepkwony *et al.*, 2001; McNeill *et al.*, 1998; Qiu and McComb, 1995; Turner and Haygarth, 2001; Venterink *et al.*, 2004). Similarly, increases in the solubilization of C and N following soil freezing and thawing are widely reported (Freppez *et al.*, 2007; Wang and Bettany, 1993; Williams and Wheatly, 1991), but there has been little research on the effects it has on P solubilization (Freppez *et al.*, 2007; Ron Vaz *et al.*, 1994). Phosphorus is particularly important as not only is it a vital nutrient for DNA, RNA, and energy transfer in all organisms, but also its importance in the eutrophication of freshwater systems is increasingly being recognized (Conley *et al.*, 2009). Consequently, a better understanding of the pools, sources, and processes affecting its cycling is vital if we are to understand how predicted climate change will affect potential loss of soil P to surface waters and how agriculture can optimize nutrient use at this time of growing concern over food security and production efficiency.

1.1. Rationale

The soil has been identified as one of the key diffuse sources of P, but the role of the various pools of P in the soil in this context is relatively unknown. Phosphorus can exist in many forms in soils, but in simple terms, it generally exists in one of the following forms: as part of recalcitrant mineral particles, in either soluble or adsorbed mineral forms such as colloidal P, or as part of soil organic matter. Both organic and inorganic P may be solubilized following drying and rewetting of soils, although organic P generally dominates (Turner and Haygarth, 2000; Turner *et al.*, 2003b). However, the sources of this P are still poorly understood. Some reports consider that the physical disruption of aggregates upon rewetting (Birch and Friend, 1958; Miller *et al.*, 2005; Powlson and Jenkinson, 1976) and subsequent solubilization of particulates and associated P are the key processes involved, while others claim that the source of solubilized P is mainly the lysis of microbial cells (Grierson *et al.*, 1998; Turner and Haygarth, 2000; Turner *et al.*, 2003b) and native soil organic matter (Jenkinson, 1966; Pulleman and Tietema, 1999; Van Gestel *et al.*, 1991). Many consequences

of the drying–rewetting process in soils are similar to those that occur during freezing–thawing cycles (Lehrsch *et al.*, 1991). Freezing can affect aggregate stability (Larson and Allmaras, 1971) resulting in increased mobilization of soil particulates upon thawing, while the expansion of intracellular fluids during freezing can result in cell lysis and release of solutes (Soulides and Allison, 1961). Physicochemical reactions involving organic matter can also occur and are similar to those during drying–rewetting episodes (Giesy and Briese, 1978).

Theoretically, drying and rewetting or freezing and thawing of soils can result in solubilization of P from any of the P pools in soils. However, there is increasing interest in one particular component of soil organic P that may be especially susceptible to such stresses, and hence constitutes a significant source of solubilizable P in many soils: the soil microbial biomass. This is the living component of soil organic matter, comprising 1–3% of the total organic matter in most soils and by definition excludes higher soil animals and plant roots (Dalal, 1998). Essentially, it comprises microorganisms in the form of bacteria, fungi, actinomycetes, and protozoa as well as nematodes. Despite the microbial biomass being a relatively small fraction of total organic matter in most soils (McNeill *et al.* 1998; Turner and Haygarth 2001), the quantities of P immobilized in the microbial biomass are surprisingly large. Brookes *et al.* (1984) estimated that in the UK the biomass P pool size in arable soils is up to 30 kg P ha⁻¹ in the plow layer, while for grassland soils, it often exceeds 100 kg P ha⁻¹. Thus the biomass P in both ecosystems can easily exceed plant P uptake, reported by Blake *et al.* (2000) as between about 5 and 30 kg P ha⁻¹ yr⁻¹ for a range of crops across Europe.

Drying and rewetting has been shown to kill up to ca. 70% of the total microbial biomass in some soils (Blackwell *et al.*, 2009a; Kieft *et al.*, 1987; Van Gestel *et al.*, 1993), and the dead biomass can act as a significant source of solubilized reactive and unreactive P. Following the air-drying of 15 different New Zealand soils, Sparling *et al.* (1985) demonstrated that the microbial biomass can contribute up to 76% of bicarbonate extractable reactive P. Turner and Haygarth (2001) examined 29 lowland pasture soils. They found a positive relationship between the quantities of microbial biomass P in the original soil and the amount of total soluble P they contained after being subjected to drying–rewetting cycles. They attributed the increases in water soluble P to P release from the microbial biomass. The large contribution of the microbial biomass to solubilized P following drying and rewetting was confirmed by Turner *et al.* (2003b) who demonstrated that up to 95% of the unreactive P solubilized following drying and rewetting of pasture soils was attributable to lysed bacterial cells. While P held in the other soil pools, such as native organic matter and colloidal P, is likely to be solubilized by abiotic perturbations, these reports suggest that, perhaps because of the dynamic nature of the soil microbial biomass, it is more vulnerable to abiotic stresses than other pools. Therefore, it could

potentially be a significant source of solubilizable P in many soils. Furthermore, any P originating from the microbial biomass has the potential for transfer from the soil to surface waters (Qiu *et al.*, 2004; Turner and Haygarth, 2001, Turner *et al.*, 2003a), where it may trigger eutrophication events.

1.2. Objective

In the current paper, we examine the evidence for the soil microbial biomass acting as a significant source of P in surface waters by reviewing the literature on the processes responsible for its solubilization and transfer, resulting from drying–rewetting and freezing–thawing processes. This is considered in light of the changes to the abiotic processes affecting microbial P solubilization, mobilization, and transfer as a result of predicted climate change. Usually, the different sources of soil-derived P in surface waters are considered *en masse*. This is because it is generally difficult to differentiate between the different sources of soil-derived P in surface waters, and even soluble P in soil itself. However, the focus here is on the release of P directly from microbial cells, either through their mortality or biological regulatory and/or metabolic processes. Waterlogging of soils can also result in microbial release of P, but generally this process is neither temporally nor spatially as extensive in soils as drying–rewetting and freezing–thawing processes and therefore is not considered here. We will highlight key gaps in the literature and discuss the research that is required to improve our knowledge. A summary of the key issues covered and how they are interrelated is shown in Fig. 1. This topic has a wide significance in that a better understanding of the processes associated with microbial P released during drying–rewetting and freezing–thawing events will assist in predicting how climate change will affect soil nutrient status and plant–nutrient interactions, the potential loss of P in leachate, and overall soil function.

2. FACTORS AFFECTING SOLUBILIZATION OF PHOSPHORUS FROM THE SOIL MICROBIAL BIOMASS

Decreases of more than two-thirds of the original microbial biomass immediately following drying of soils have been reported (Blackwell *et al.*, 2009a; Bottner 1985; Kieft *et al.*, 1987; van Gestel *et al.*, 1993). Logsdail and Webber (1959) reported that most of the bacteria were eliminated in a soil subjected to a sudden, severe frost, while Soulides and Allison (1961) reported that freezing can decrease soil bacterial numbers by up to a third. The basic processes involved in reducing the microbial populations in soils following these perturbations are well documented.

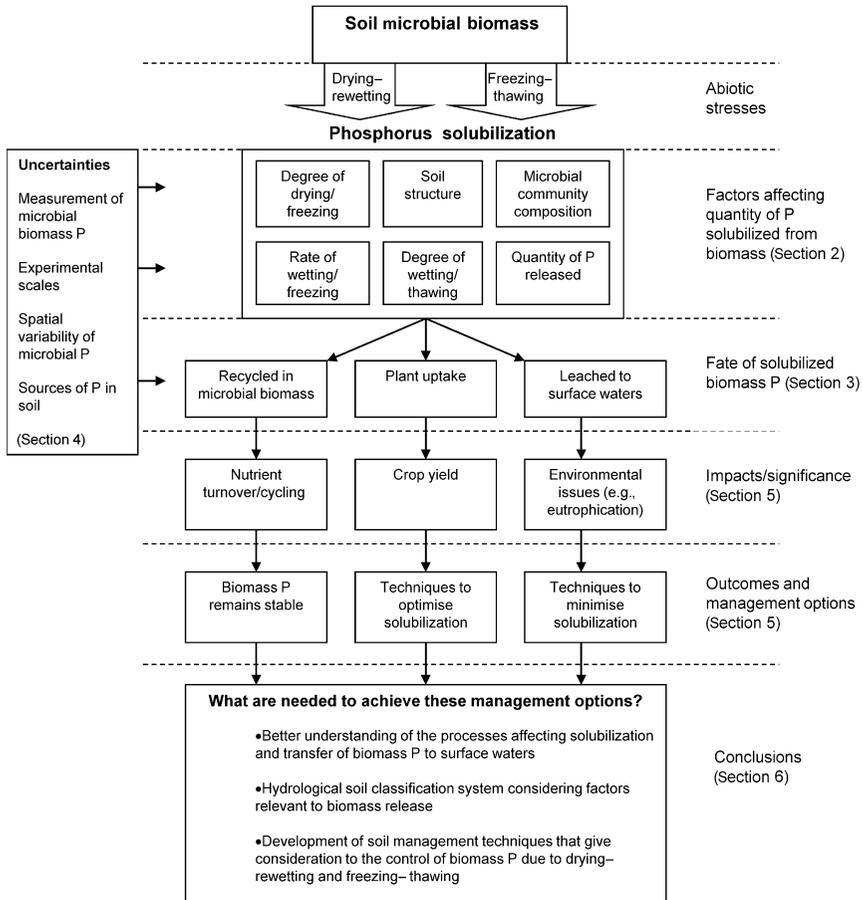


Figure 1 Summary of key factors affecting the solubilization of P from the soil microbial biomass by abiotic processes.

2.1. Primary solubilization processes

At the microbial scale, the main processes by which drying-rewetting and freezing-thawing cycles directly affect soil microorganisms are desiccation, osmotic processes, cell lysis and intracellular fluid expansion upon freezing and cell disruption.

2.1.1. Desiccation, osmotic regulation and osmotic shock

Desiccation, osmotic regulation and osmotic shock occur largely due to the stresses imposed by changes in soil water potential. In simple terms, soil water potential is a measure of the energy required to remove water from

the soil. Soil drying is generally a gradual process during which turgor pressure increases as water is removed from the surrounding soil and so the microbial cells release water (generally thought not to contain P) in order to equilibrate this pressure (homeostatic regulation). This means that mortality and cell lysis do not necessarily occur, although if too extreme, desiccation, and mortality will take place (Halverson *et al.*, 2000), resulting in the release of microbial P. Similarly anhydrobiosis occurs in some microorganisms in an attempt to avoid damage during freezing. In this process, bulk water within cells is minimized or even eliminated, leaving behind only miniscule amounts of water forming bound or vicinal water shells around macromolecules, resulting in no free water to form damaging ice crystals (see below), but severe desiccation can occur, again potentially leading to P solubilization (Storey and Storey, 2005). Increases in solute concentrations in the soil solution can occur during drying due to the evaporation of water, while during freezing this increase results from the removal of pure water from the soil solution to form ice crystals in the extracellular spaces, rather than in the cell itself. Both processes set up a steep osmotic gradient across cell membranes causing an outflow of water and consequently cell dehydration, elevated intracellular ionic strength and cell volume reduction, all of which cause stress and potential death. The rewetting of dry soils can cause rapid fluctuations in soil matric potential ranging from -20 MPa to almost 0 (Evans *et al.*, 1975), causing a number of different microbial processes to occur. Rapid increases in turgor pressure can occur, resulting in cell damage, plasmolysis and/or death (Harris, 1981; Kieft *et al.*, 1987; Salema *et al.*, 1982; Storey and Storey, 2005). This results in the release of cell contents of which P is an important component. However, the thicker a microorganisms cell wall, the more likely it is to be able to withstand these pressures (Harris, 1981). Halverson *et al.* (2000) report that, upon rapid rewetting, cells may actively or passively release intracellular organic and inorganic solutes (Christian, 1962; Reed *et al.*, 1986), as well as catabolize compatible organic solutes to CO_2 or polymerize solutes to reduce osmotic activity (Berrier *et al.*, 1992; Fierer and Schimel, 2003; Reed and Stewart, 1983), thereby avoiding cell lysis and mortality. The chemistry of the rewetting water is also important because if it is not in ionic balance with intracellular solutions this can also increase the likelihood of osmotic shock (Appel, 1998).

2.1.2. Intracellular fluid expansion upon freezing and cell disruption

When ice crystals form they can cause direct physical damage to cells and tissues. Shearing and squeezing stresses can break individual cells trapped among growing ice crystals resulting in cell rupture, and subsequent release of P-containing cytoplasm upon thawing (Storey and Storey, 2005). When ice crystals form inside cells, subcellular architecture can be damaged and

metabolic pathways can be disrupted, again resulting in cell lysis and death (Edwards and Cresser, 1992). However, the degree to which this occurs will depend on the chemical composition of the cytoplasm, as psychrophiles (organisms able to grow at low temperatures) have developed a number of ways of surviving in frozen soils including the production of biomolecules enabling them to function at low temperatures (Madigan *et al.*, 2000; Robinson, 2001; Storey and Storey, 2005).

2.2. Thresholds of solubilization

The degree, rate, and duration of soil drying and rewetting can vary, as can the quantity and chemistry of the rewetting water, all of which can affect microbial responses. Similarly, whether a soil is frozen slowly or rapidly, the minimum temperature, duration of freezing and the number of freeze–thaw events can result in different effects on the soil microbial biomass. All these factors can affect the degree to which the microbial biomass is impacted and the quantity of P released.

2.2.1. Drying–rewetting

The longer a soil remains dry, the less the ability of the biomass to recover upon rewetting, at least in the short term (De Nobili *et al.*, 2006). After 12 years the period of drying was found to make little difference. This has implications for the biomass in regions where droughts can last for several years, and if these become extended, possibly as a result of climate change, biomass populations may become severely depleted. The rate at which a soil dries and rewets affects the stress experienced by organisms, it being both a function of the absolute water potential value and the rate of change of water potential. Slow drying of soil can enable microbial metabolic adjustment which reduces mortality during the drying process (Chao and Alexander, 1984; Roberson and Firestone, 1992). The degree of drying is also important as shown by Kieft *et al.* (1987), who reported greater biomass mortality upon the rewetting of soils dried to -6.9 MPa compared to -2.8 MPa. West *et al.* (1992) found that biomass remained constant until soil moisture dropped to between 0.1 and $0.3 \text{ m}^3 \text{ m}^{-3}$, but reported that the rates at which soils dry do not affect biomass survival, despite differences in soil texture, organic matter and moisture characteristics. Rate of drying is closely related to the temperature at which drying takes place. Turner and Haygarth (2001) found that while the temperature at which soils were dried did not affect the total quantity of P solubilized, it did affect the rate of solubilization. At higher temperatures the biomass was killed more quickly making microbial P available in soils more rapidly than under drying at lower temperatures. Again this has implications for changes in patterns of drying and rewetting under climate change, with a predicted shift towards higher temperatures. This implies that microbial P will potentially be more

rapidly solubilized, but whether or not it increases the likelihood of leaching will depend upon the nature of rewetting, as discussed in [Section 3](#). The fact that the P is more rapidly available could mean that there is greater opportunity for it to be utilized by other soil organisms or plants, thereby reducing its potential loss.

Soil rewetting usually takes place rapidly following precipitation, irrigation, or flooding as a wetting front penetrates the soil. This can exert some of the greatest stresses experienced by soil microorganisms ([Kieft *et al.*, 1987](#)). If the drying phase of a soil is relatively slow, osmotic regulation can take place resulting in only a small change in biomass. Hypothetically, if the rewetting process occurs at a slow rate, then solubilized nutrients from either the biomass or other sources could potentially be taken up by the surviving microbes, stimulating microbial growth, and the biomass would be restored to almost its original status. However, at the microbe scale, slow rewetting is unlikely to occur as most rewetting processes are not subtle enough to constitute slow rewetting. One possible exception is if a soil is rewetted through the introduction of water vapour, which slowly condenses. Therefore, during most rewetting events osmotic shock occurs and some microbes die, resulting in a rapid decrease in biomass and release of microbial P. When rewetting a dried soil at rates ranging from 0 to 48 h, [Blackwell *et al.* \(2009a\)](#) found that the rate of rewetting had no significant effect on the quantity of microbial biomass, thereby supporting this speculation.

The frequency of drying–rewetting cycles is also an important factor in determining the release of biomass P. In experiments where soils were subjected to repeated drying–rewetting cycles, some researchers have reported contrasting results. Almost full recovery of biomass following initial depletions of up to one third the original biomass were found by [Bottner \(1985\)](#) while [Butterly *et al.* \(2009\)](#) found that microbial biomass P and C concentrations were gradually depleted. They both observed a reduction in activity following an initial increase, which they attributed to an initial rapid turnover of microbial nutrients during the first few drying–rewetting cycles, during which the microbial communities adapt to the variable conditions and indeed the community changes (see [Section 2.3](#)), such that the effects of drying and rewetting are reduced with regard to cell mortality as more resilient species dominate ([Franzuebbers *et al.*, 1994](#); [Lundquist *et al.*, 1999](#); [Mikha *et al.*, 2005](#)). Additionally, the active fraction of the biomass is likely to be depleted, so although no shift in community or biomass may be observed, the change in activity could potentially reflect a change in the inherent properties of the population ([van Gestel *et al.*, 1993](#)). In contrast, [Miller *et al.* \(2005\)](#) detected a negligible decrease in activity following repeated rewetting of chaparral soils despite decreases in total soil C, although the frequency of drying and rewetting was identified as an important factor controlling the amount of CO₂ emitted during rewetting episodes.

The translocation of water by roots may also cause localized drying–rewetting within soils and therefore, diffused microsite drying–rewetting cycles may occur, in addition to the larger drying–rewetting cycles associated with precipitation, irrigation, and flooding events. Murray *et al.* (2006) observed reductions in soil microbial biomass in soils which had received N fertilizer. They speculated that this was caused by soil drying due to increased evapotranspiration by the larger plants resulting from fertilizer application. It is likely that most soils will be adapted to these microvariations and it is probably the larger, more extreme events that would result in mobilization and leaching of biomass P.

2.2.2. Freezing and thawing

Soulides and Allison (1961) found that repeated freezing of an air-dried temperate soil did not kill bacterial cells, but that one treatment was sufficient to eliminate most of the organisms that were unable to withstand the impact of freezing. They also reported that, as for drying of soils, the rate of bacterial destruction by freezing was highest when bacteria was in its growth stage and almost negligible during the decline stage. Feng *et al.* (2007) also found that repeated freeze–thaw cycles did not significantly affect bacterial populations, but did cause a gradual decline in fungal biomass, while Sjurson *et al.* (2005) observed that extended periods of freezing did not affect the fungal biomass, but did cause a decline in bacterial populations. The rate at which a soil freezes is also important because it not only affects the size of ice potentially damaging ice crystals, but can also affect the opportunity the microbial biomass has to adapt to the changing conditions. At high freezing rates ($> 1.4 \text{ }^\circ\text{C h}^{-1}$) decreases in biomass have been reported, while at relatively lower freezing rates, they remain unaffected (Lipson *et al.*, 2000). This could be because slower freezing rates mean microbes have more opportunity to purposely dehydrate (anhydrobiosis), thereby removing all bulk water which potentially could cause harm during freezing (Storey and Storey, 2005). Similarly during moderate freeze–thaw treatments many soil microbes are able to survive both single and multiple freeze–thaw cycles (Grogan *et al.*, 2004), but not single severe freezing, when temperatures fall below $-10 \text{ }^\circ\text{C}$ (Mikan *et al.*, 2002; Soulides and Allison, 1961). This is because while bulk soil water freezes below $0 \text{ }^\circ\text{C}$, soil particles continue to have thin liquid films around them in which microbes not only survive, but also continue activity typically down to $-10 \text{ }^\circ\text{C}$, but sometimes down to $-40 \text{ }^\circ\text{C}$ (Romanovsky and Osterkamp, 2000; Schimel and Mikan, 2005). The duration of freezing is also likely to be important, because as the freezing period is extended, soil aggregates will become increasingly dehydrated as water is drawn towards the freezing front. Sometimes a freezing front will move progressively down through a soil profile, with the excluded solutes becoming increasingly concentrated and having implications for osmotic processes (see above). Edwards *et al.* (2006)

reported that in boreal soils a large and rapid (7–10 days) decrease in microbial biomass occurred following thawing of soils maintaining temperatures around 0 °C. They attribute this primarily to competition for nutrients from plants becoming active at these temperatures. Similar observations were made by [Larson *et al.* \(2007\)](#) in subarctic soils. Thus it would appear that in soils accustomed to low temperatures it is extreme freezing events and extended periods of defrosting that are most detrimental to the biomass, while repeated, moderate freeze–thaw cycles have less effect. In contrast, single moderate freezing events are significantly detrimental to the biomass in temperate soils. However, temperature threshold values for specific soils and processes cannot be defined ([Matzner and Borken, 2008](#)).

2.3. Impacts on microbial communities

Different groups and species of microorganisms react differently to varying degrees, duration, and frequency of desiccation and freezing. Most microorganisms are capable of surviving periods of desiccation form endospores, cysts, or other resistant structures, whereas *Arthrobacter* and some rod-shaped bacteria can survive drying as more-or-less structurally unmodified cells ([Chen and Alexander, 1973](#)). Similar methods are adopted by various microorganisms to survive freezing, with many forming spores that germinate upon thawing, while others dehydrate to avoid the damaging effects of ice crystal formation. Some have developed the ability to produce antifreeze agents, so that they can survive much colder temperatures ([Robinson, 2001](#); [Storey and Storey, 2005](#)). The dominant varieties of soil microorganisms are therefore likely to affect the quantity and form of biomass P released. For example, those forming cysts or spores are likely to release both cell wall and cytoplasm P compounds from the parent cell. [Figure 2](#) illustrates a simplified version of the processes that may occur and how P can be mobilized from soil microbes during a drying–rewetting cycle. In [Fig. 2A](#), soil microbes are fully hydrated in a moist soil, and P is present in the cytoplasm and cell walls of intact cells. In [Fig. 2B](#) the soil undergoes drying so that desiccation occurs, cells rupture and P is released into the soil solution and cell walls become part of the soil organic matter. In [Fig. 2C](#) the soil, undergoes drying, but cells osmoregulate and survive, releasing no microbial P. In [Fig. 2D](#) the soil undergoes rewetting, and some of the P released during desiccation is taken up by other and new soil microbes. Some P remains in the soil solution and P in the cell walls of dead microbes is incorporated into the soil organic matter. In [Fig. 2E](#) the soil undergoes rapid rewetting, causing osmotic shock and cell lysis. Phosphorus is released into the soil solution and cell walls form part of the soil organic matter. Finally, in [Fig. 2F](#) the soil undergoes slow rewetting, cells remain intact and rehydration occurs. This final scenario is unlikely but could possibly occur, as discussed above.

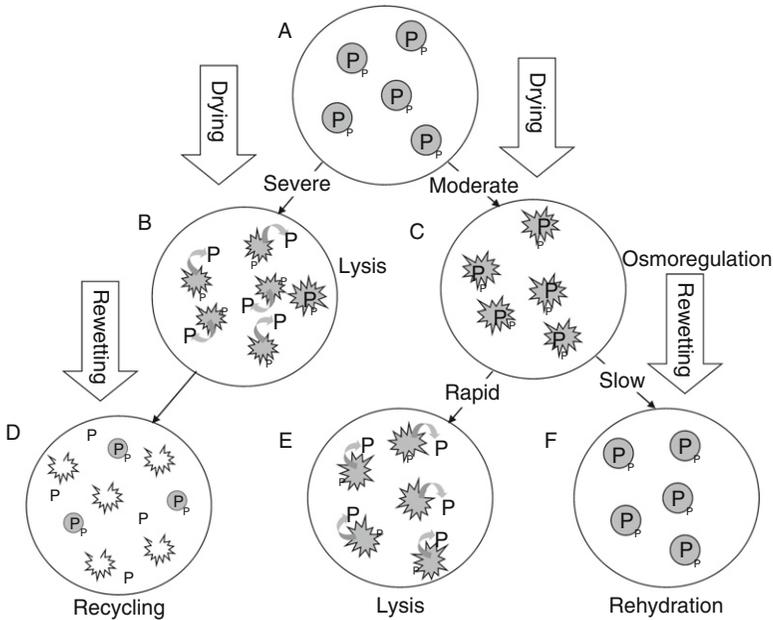


Figure 2 Simple diagram of the effects of drying–rewetting events on the soil microbial biomass and potential for P solubilization.

In addition to the type of microbial populations present, the inherent properties of the biomass, such as physiology and metabolic state, can also affect responses to perturbations. [Soulides and Allison \(1961\)](#) found that cells in a sporulated or resting state are less susceptible to drying or freezing than rapidly growing cells, while [Bottner \(1985\)](#) and [van Gestel *et al.* \(1993\)](#) reported that active biomass is more vulnerable to drying than the dormant fraction.

Following rewetting, different microorganisms may have a reproductive advantage over others depending on various factors. For example, extreme desiccation may favour gram-positive bacteria and fungi, which are more likely to survive such events but are slow-growing, while less extreme events may favour organisms such as gram-negative bacteria. These are able to multiply more rapidly due to the increased availability of nutrients ([Bushby and Marshall, 1977](#); [Fierer *et al.*, 2003](#)), but are more susceptible to drying ([van Gestel *et al.*, 1993](#)). Fungi are generally reported to be more susceptible to freezing than bacteria ([Feng *et al.*, 2007](#)), but this does vary depending upon the temperature, rate, and duration of freezing. Such differences imply that drying–rewetting and freezing–thawing cycles will cause changes in soil microbial communities, but that these changes will to some extent be dependent on the characteristics of drying and freezing. While some

evidence exists to show that community shifts can occur (Feng *et al.*, 2007; Gordon *et al.*, 2008; Lundquist *et al.*, 1999), for example yeasts recolonize the soil more successfully than filamentous fungi and bacteria (Sparling and Cheshire, 1979), it is not always the case. Rather, it depends largely on whether soils regularly experience drying–rewetting or freezing–thawing events and if the microbial community is adapted to such conditions (Fierer *et al.*, 2003; Griffiths *et al.*, 2003; Hamer *et al.*, 2007; Koponen *et al.*, 2006). Additionally, drying–rewetting and freezing–thawing cycles are likely to cause a shift in the inherent properties of the microbial population with a trend towards greater survival of less active, more mature organisms (Bolter *et al.*, 2005; Soulides and Allison, 1961; van Gestel *et al.*, 1993), which will be less susceptible to further perturbations (see above). Figure 3 shows how microbial community changes may occur due to drying and rewetting within a single soil aggregate. Figure 3A shows a moist aggregate with equal numbers of gram-positive and gram-negative bacterial cells and fungi. In Fig. 3B, the aggregate experiences an extreme drying event. All gram-negative bacterial cells die due to their inability to survive extreme drying, and some

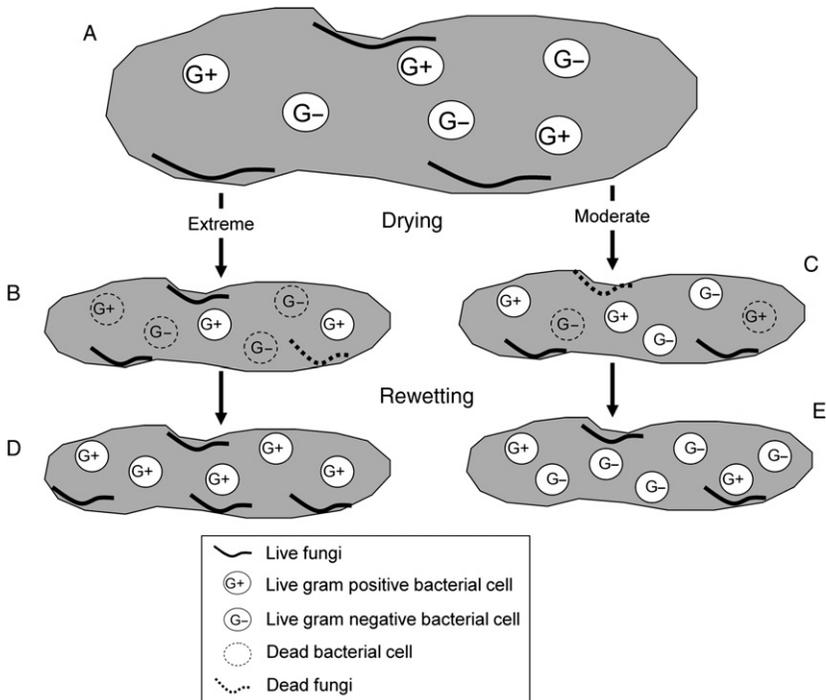


Figure 3 Possible effects of drying–rewetting events on soil microbial communities.

gram-positive bacterial cells and fungi also die. In Fig. 3C, the aggregate experiences a moderate drying event. Some of the three types of microorganisms die and some of the three types also survive. Figure 3D shows, that upon rewetting, gram-positive bacteria and fungi reproduce using nutrients released by the dead gram-negative cells, and gram-positive bacteria and fungi dominate. Figure 3E shows that upon rewetting, surviving gram-negative bacterial cells are able to regenerate more rapidly than gram-positive bacterial cells and fungi, and consequently gram-negative bacteria dominate.

3. FACTORS CONTROLLING TRANSFER TO SURFACE WATERS

3.1. Internal cycling of phosphorus

There is substantial evidence indicating that after a soil experiences a perturbation, the rate of microbial turnover and activity increases, probably as a result of the recycling and processing by the surviving biomass of nutrients released from the original biomass and other sources. Many studies have considered the observed pulse of CO₂ emission from soils following rewetting (Birch, 1958; Bottner, 1985; Butterly *et al.*, 2009; Fierer and Schimel, 2003; Mikha *et al.*, 2005; Miller *et al.*, 2005) and thawing (Schimel and Clein, 1996; Soulides and Allison, 1961) as an indicator of microbial activity. The actual processes involved have been topics of great debate. Originally it was thought that physical soil processes could explain these flushes of activity, whereby desiccation and freezing of soil organic matter resulted in exposure to enzymes of previously inaccessible surfaces of organic or organo-mineral colloids due to aggregate fragmentation or increased porosity (Birch, 1958; Soulides and Allison, 1961). Powlson and Jenkinson (1976) confirmed that the physical disruption of the soil structure and substrate desorption from surfaces along with increased microbial mobility, all caused by drying-rewetting cycles, increases the solubilization of organic compounds including organic P. Similar results are reported by Dergacheva and Dedkov (1977) and Giesy and Briese (1978) following freezing-thawing of soils. However, despite being a relatively small fraction of the total organic matter found in most soils, the microbial biomass is potentially one of the main sources of P solubilized after such stresses.

Significant decreases in soil microbial biomass following drying have been reported, (Blackwell *et al.*, 2009a; Bottner 1985; Kieft *et al.*, 1987; van Gestel *et al.*, 1993), but evidence for the recovery of biomass following rewetting is varied. Grierson *et al.* (1998) reported increased biomass P in a spodosol 28 days after a drying-rewetting event, while Mondini *et al.* (2002) observed that biomass in a soil did not recover to original, predrying conditions 12 days