

# Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils

WERNER BORKEN and EGBERT MATZNER

*Department of Soil Ecology, University of Bayreuth, 95440 Bayreuth, Germany*

## Abstract

In the next decades, many soils will be subjected to increased drying/wetting cycles or modified water availability considering predicted global changes in precipitation and evapotranspiration. These changes may affect the turnover of C and N in soils, but the direction of changes is still unclear. The aim of the review is the evaluation of involved mechanisms, the intensity, duration and frequency of drying and wetting for the mineralization and fluxes of C and N in terrestrial soils. Controversial study results require a reappraisal of the present understanding that wetting of dry soils induces significant losses of soil C and N. The generally observed pulse in net C and N mineralization following wetting of dry soil (hereafter wetting pulse) is short-lived and often exceeds the mineralization rate of a respective moist control. Accumulated microbial and plant necromass, lysis of live microbial cells, release of compatible solutes and exposure of previously protected organic matter may explain the additional mineralization during wetting of soils. Frequent drying and wetting diminishes the wetting pulse due to limitation of the accessible organic matter pool. Despite wetting pulses, cumulative C and N mineralization (defined here as total net mineralization during drying and wetting) are mostly smaller compared with soil with optimum moisture, indicating that wetting pulses cannot compensate for small mineralization rates during drought periods. Cumulative mineralization is linked to the intensity and duration of drying, the amount and distribution of precipitation, temperature, hydrophobicity and the accessible pool of organic substrates. Wetting pulses may have a significant impact on C and N mineralization or flux rates in arid and semiarid regions but have less impact in humid and subhumid regions on annual time scales. Organic matter stocks are progressively preserved with increasing duration and intensity of drought periods; however, fires enhance the risk of organic matter losses under dry conditions. Hydrophobicity of organic surfaces is an important mechanism that reduces C and N mineralization in topsoils after precipitation. Hence, mineralization in forest soils with hydrophobic organic horizons is presumably stronger limited than in grassland or farmland soils. Even in humid regions, suboptimal water potentials often restrict microbial activity in topsoils during growing seasons. Increasing summer droughts will likely reduce the mineralization and fluxes of C and N whereas increasing summer precipitation could enhance the losses of C and N from soils.

**Keywords:** C mineralization, drying, nitrate leaching, N mineralization, precipitation, soil moisture, soil organic carbon, soil respiration, wetting

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## Introduction

Based on model simulations, it is likely that soil moisture will decrease in most regions of the earth during

Correspondence: Werner Borken, tel. + 49 921 555741, fax + 49 921 555799, e-mail: werner.borken@uni-bayreuth.de

this century (Meehl *et al.*, 2007). Particularly, mean annual soil moisture is expected to decrease up to 25% in the subtropics and the Mediterranean region. A globally increasing likelihood of severe drought periods will cause irregular and extreme water stress for soil organisms and plants. Even in regions with increasing annual amounts of precipitation, increasing

evapotranspiration or shifts in precipitation pattern could constrain the availability of soil water during growing seasons. These climatic changes may have implications for nutrient availability, plant productivity, biogeochemical processes, gaseous and leaching losses and, possibly in the long run, for C and N pools in soils.

While arid, semiarid and Mediterranean ecosystems are adapted to extreme droughts (Austin *et al.*, 2004), ecosystems of other climatic zones generally experience less severe and shorter periods of water shortage. Nevertheless, exceptional rain deficits will have a strong impact on plant productivity as observed in the summer of 2003 in many European regions. Ciais *et al.* (2005) stressed that such extreme drought events could reverse some forest ecosystems from carbon sinks to transient net carbon sources. This whole-ecosystem switch from a carbon sink to a carbon source, however, is not necessarily transferable to soils because soil microorganisms may respond to drought in a different way than plants. A previous study suggests that temperate forest soils may become at least a transient net sink for organic carbon in years with extended summer droughts, because the decay of soil organic matter was stronger reduced than rhizosphere respiration (Borken *et al.*, 2006). Many plants have a limited ability to sustain their metabolism during drought periods through water uptake from groundwater or moist soil horizons while most soil microorganisms are directly exposed to water stress in topsoils. On the other hand, only microorganisms located in the topsoil may profit from small precipitation events during drought periods (Huxman *et al.*, 2004a,b), triggering a transient asynchrony in mineralization and nutrient uptake by plants.

It has been well documented that in most cases drying of soil reduces and subsequent wetting rapidly enhances the microbial activity in soils (e.g. Birch, 1958a; Bottner, 1985; Van Gestel *et al.*, 1993a). The response of microbial processes to these disturbances, however, is possibly not only related to soil moisture and the accessibility of nutrients and soil organic matter, but also to changes in the bacterial community structure (Fierer *et al.*, 2003) and in the stability and formation of soil aggregates (Denef *et al.*, 2001a,b). Moreover, specific microbial processes may exhibit different sensitivities to soil moisture. For example, nitrification in coniferous litter linearly declined with decreasing gravimetric water content whereas C mineralization was only slightly affected at water contents between 75% and 300% (Tietema *et al.*, 1992).

A large number of laboratory studies have been performed during recent decades to understand the mechanisms and to assess changes in microbial structures and mineralization rates during drying and wetting. However, results from laboratory studies are

inconsistent probably because of varying experimental designs, incubation temperatures, soil properties and treatments. The few field studies on this topic mostly simulated reduced rainfall (Hanson *et al.*, 2003; Davidson *et al.*, 2004; Yahdjian *et al.*, 2006; Sotta *et al.*, 2007) or single, extreme drought periods followed either by natural wetting or artificial wetting (Borken *et al.*, 1999, 2006; Emmett *et al.*, 2004). Other approaches are the experimental increase in precipitation that allows the evaluation of natural drought events (Bloem *et al.*, 1992; Matson *et al.*, 1992; De Visser, 1995; De Visser & van Breemen, 1995; Hanson *et al.*, 2003) or the analysis of field observations (e.g. Jarvis *et al.*, 2007). Similar to the laboratory results, contradictory conclusions were drawn from the field measurements.

In the long run, substantial changes in precipitation and evaporation may affect some soil functions such as the mineralization and sequestration of soil organic matter. In this review, we analyse the literature on the effects of drought and subsequent wetting on C and N mineralization or fluxes in soils from all climate regions. The following aspects will be addressed: (1) involved mechanisms during drying and wetting of soils, (2) effects of drying and wetting intensity and duration, (3) effects of drying and wetting frequency and (4) relevance for C and N losses from soils.

### Involved mechanisms during drying of soils

In this paper, we define the drying of soils as a reduction in the water content or water potential below field capacity. Soil drying is strongly influenced by air humidity, temperature, wind and transpiration and often begins shortly after rain as a result of the water deficit of air. The influence of soil drying on microbial activity is mostly restricted at elevated temperatures while the influence is rather small at low temperatures. Apart from a small optimum range, slightly below field capacity at about  $-50\text{ kPa}$ , microbial activity generally decreases in aerated soils or in litter with decreasing water potential (e.g. Orchard & Cook, 1983; Moore, 1986; Skopp *et al.*, 1990; Voroney, 2007). This relationship implies that low water potential is a common limitation of microbial activity in soils up to total inhibition under extremely dry conditions. Several mechanisms have been proposed to explain the decrease in microbial activity during drying of soils. Drought-induced changes of the physical soil structure have no direct effect on microbial activity during the drying process but may affect C and N mineralization following wetting of soil.

### Response of microorganisms

Because soil microorganisms have semipermeable membranes and live in water films (bacteria) or are

mostly in contact with water films (fungi), water potential is equilibrating between the water phase and the cytoplasm of the microbial cell. When soil is drying, the matric potential as well as the osmotic potential become more negative in soil solution. Microorganisms may dehydrate and decrease osmotic potential in the cell by accumulation of compatible solutes such as amino acids, carbohydrates, polyols and inorganic solutes to equilibrate with their environment (Harris, 1981; Halverson *et al.*, 2000). According to Harris (1981), drought stress is defined as the accumulation of compatible solutes in microbial cells.

Osmotic regulation is constrained to a certain threshold and varies among microorganisms. When the threshold is exceeded, microorganisms further dehydrate and die (Sparling & Ross, 1988; Van Gestel *et al.*, 1992, 1993b) or survive the drought period by forming endospores, cysts or vegetative cells (Chen & Alexander, 1973). Air-drying at 40 °C over 24 h killed up to one-third of the microbial biomass in a Mediterranean grassland soil (Bottner, 1985). Similarly, Sparling *et al.* (1986) reported a decrease of 14–30% in microbial biomass following air-drying. In contrast, air-drying over 14 days reduced microbial biomass by only 10% in organic and mineral horizons of an aspen and pine forest (Scheu & Parkinson, 1994), suggesting that these microorganisms were well-adapted to water stress.

The decrease in microbial biomass during drying is likely to be correlated with the duration of drying. Microbial biomass in birch litter was reduced more strongly during a 2-week drought than during shorter droughts (Schimel *et al.*, 1999). The tolerance of microorganisms to drought stress is not strongly related to their taxonomy although fungi are considered to be better adapted to drought stress than bacteria (Harris, 1981). It seems that even nonspore-forming bacteria may survive under extremely dry conditions for extended periods of time and that the tolerance of bacteria is greater when grown under stress (Chen & Alexander, 1973). Some bacteria and fungal hyphae create their own environment by secretion of mucilage consisting of polysaccharides that protect against desiccation and predation. This strategy consumes energy and carbon resources but enhances the survival of microorganisms during periods of drought stress (Schimel *et al.*, 2007).

The mechanistical response of microorganisms to increasing drought stress is, in principle, well understood. Uncertainties still exist concerning the adaptation of microbial communities and their effects on process rates in different soils and land-use systems. Particularly, the sensitivity of microorganisms and processes involved in the N cycle (ammonification, nitrification, denitrification, immobilization) to drought stress is largely unknown and requires further research.

### *Diffusive limitations*

Drying of soils reduces the availability of organic and inorganic soluble substrates and the mobility of extracellular enzymes. The diffusive transport of substrates and extracellular enzymes, as well as the active or passive mobility of microorganisms slows down with decreasing water potential and abating thickness of the water film. At very low matric potential, discontinuous water films inhibit the diffusive transport of solute substrates. According to Voroney (2007), the decrease in microbial activity can be attributed to two simultaneously occurring mechanisms – osmotic regulation and limited diffusive transport. The study by Stark & Firestone (1995) on the effect of soil moisture on the activity of nitrifying bacteria suggests that substrate limitation is the dominating factor when osmotic potentials are greater than  $-0.6$  MPa, whereas cell dehydration is the major inhibiting factor when osmotic potentials decrease below  $-0.6$  MPa. In the same study, the nitrification rate strongly declined by about 40% following mild drying of moist soil from  $-0.01$  to  $-0.2$  MPa. Similarly, Ford *et al.* (2007) reported negligible C and N mineralization for semiarid grassland soils dried to  $-1.0$  MPa. They concluded that substrate and water availability are more important for process rates than the substrate quality or composition of microbial community.

### *Belowground allocation of organic substrates*

At ecosystem level, the availability of organic substrates is further constrained by the reduction in root growth and exudation during drought. Drought manipulations in different shrubland ecosystems reduced the flow of soluble carbon from the root system into the soil and the microbial biomass by more than 60% (Gorissen *et al.*, 2004). In a spruce forest, fine root biomass seemed to decrease in the topsoil and to increase in the subsoil owing to drought manipulation (Persson *et al.*, 1995). This implies that C input by roots is partly interrupted in the topsoil during dry periods. Because symbiotic fungi and many free-living microorganisms depend on the C transfers from roots, microbial CO<sub>2</sub> production is consequently reduced in the rhizosphere during drought periods.

### *Changes in soil structure*

Low soil moisture causes changes in the soil structure and induces hydrophobicity of soil surfaces, but these changes have presumably no direct effect on C and N mineralization during drought periods. The physical disruption of macro- and microaggregates by shrinking

may lead to the exposure of new soil surfaces and of previously protected organic matter (Utomo & Dexter, 1982; Appel, 1998; Denef *et al.*, 2001a). The intensity of soil shrinking and aggregate stability is related to the kind of clay minerals, clay and organic matter contents and microbial biomass (Haynes & Swift, 1990; Denef *et al.*, 2001b; Peng *et al.*, 2007).

Additionally, soil shrinking affects the size and stability of pores, being most pronounced in organic soils and forest floors with large portion of macropores. Macropores have less cohesion than micropores because small capillary stress diminishes the contraction of soil particles, organic matter and aggregates (Peng & Horn, 2005). Thus, soil macropores and macroaggregates are preferentially destabilized during drying. In clayey soils, however, the stability of micropores increases with drying due to the cohesion of slightly soluble components with soil particles (Kemper & Rosenau, 1984). Whether destabilizing or stabilizing aggregation processes dominate will most likely be a result of pore-size distribution, the amount and quality of cohesive and water-repellent substances.

#### *Hydrophobicity of soil surfaces*

Hydrophobicity of soil surfaces caused by organic substances increases with the intensity of drying and has a large impact on microbial activity during wetting. The extent of hydrophobicity of a specific soil is controlled by soil moisture and the history of drying and wetting, complicating the determination of general thresholds for soil hydrophobicity (Doerr & Thomas, 2000). Because hydrophobicity is linked to the amount of soil organic matter (Mataix-Solera *et al.*, 2007), it regularly occurs in the organic layer of forest soils during dry summers and may persist over weeks or even months. In mineral soils, hydrophobicity is generally less pronounced due to smaller organic matter contents, but in arid, semiarid and Mediterranean regions it largely affects the hydrology of soils. Water repellence is attributed to aliphatic constituents of organic compounds or hydrophobic substances like waxes (e.g. Piccolo & Mbagwu, 1999; Franco *et al.*, 2000; Verheijen & Cammeraat, 2007). Not only plant litter but also soil fungi have been considered to enhance the hydrophobicity of soils by production of extracellular polysaccharides and hydrophobic substances (Cosentino *et al.*, 2006).

Many organic compounds have both hydrophobic and hydrophilic constituents; the latter being attracted to mineral surfaces or other hydrophilic organic constituents through van der Waals interaction during drying. The hydrophilic constituents are bonded and thereby ineffective to interact with water molecules

while the hydrophobic constituents provide a water-repellent coating (Doerr *et al.*, 2000, 2007).

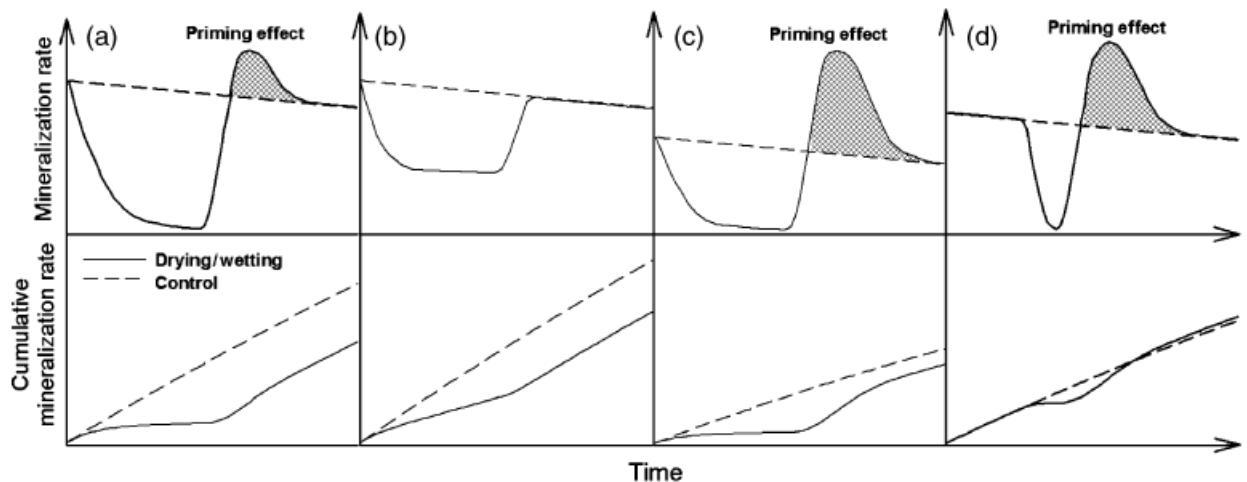
In summary, changes in hydrophobicity and aggregate stability are likely of minor importance for microbial activity during desiccation as compared with osmotic regulation and diffusive transport. Nonetheless, these mechanisms can have a great influence on C and N mineralization during wetting of dry soils as outlined below. It is also noteworthy, that hydrophobicity increases the risk of organic matter losses by natural fire (Certini, 2005). Losses can be high in boreal forests when large amounts of dry organic matter are stored in forest floors.

#### **Mechanisms during wetting of dry soils**

Wetting of dry soils generally increases the microbial activity within minutes (Borken *et al.*, 2003; Lee *et al.*, 2004; Sponseller, 2007) or hours (Pulleman & Tietema, 1999; Prieme & Christensen, 2001). This wetting pulse may be attributed to (1) reconstituting mineralization of soil organic matter and (2) to the mineralization of previously unavailable, easily decomposable organic substrates (e.g. van Gestel *et al.*, 1991; Appel, 1998; Wu & Brookes, 2005). The latter may cause an extra short-term boost in microbial activity for a few days that exceeds the microbial activity of a permanently moist soil (Fig. 1a). This priming effect has recently been termed as the 'Birch effect' to acknowledge Birch's pioneering work (e.g. Birch, 1958a,b, 1964) on drying and wetting effects in soils (Jarvis *et al.*, 2007). The organic substrates causing this priming effect may originate from different sources produced, accumulated or exposed during the drying period. Wetting of a dry soil, however, may induce further mechanisms that enhance the availability of organic substrates.

#### *Release of microbial biomass*

Wetting of dry soils triggers the hydration and lysis of dead microbial cells, which accumulate during drying periods. These substrates may subsequently be metabolized by surviving microorganisms. Surviving microorganisms, however, may experience even more stress than during the drying period and possibly die following wetting (Schimel *et al.*, 2007). If microorganisms do not rapidly equilibrate to sudden changes in water potential by disposing their compatible solutes, water will flow into the cytoplasm and destroy the cell unless the cell wall resists the turgor pressure (Kieft *et al.*, 1987). The equilibration to the water potential may include the metabolic decay or the polymerization of compatible solutes into osmotically less active compounds, as well as the passive and active export from



**Fig. 1** Potential C and N mineralization in soils following drying and wetting scenarios: (a) moderate wetting pulse (priming effect) relative to an optimal moist control, (b) recovery of mineralization (no priming effect) relative to an optimal moist control, (c) strong wetting pulse (pseudo-priming effect) relative to an suboptimal moist control, and (d) short drying period and enhanced wetting pulse (pseudo-priming effect) relative to a suboptimal moist control.

the cell into the soil solution (Halverson *et al.*, 2000). Kieft *et al.* (1987) reported for grassland soils that 17–70% of total microbial biomass C were released by rapid wetting. The release of biomass C increased with the magnitude of change in water potential and varied between two grassland soils. In contrast, small amounts of released microbial proteins and DNA suggest that an increase in water potential from  $-3.0$  to  $-1.0$  MPa causes almost no cell lysis (Halverson *et al.*, 2000). In agreement with this study, Fierer & Schimel (2003) found no evidence for microbial cell lysis in rewetted soils from an oak forest and grassland. The contradictory study results might be due to differences in the physiological state of soil microorganisms. Active microorganisms are more likely to be susceptible to drying and wetting stress than dormant microorganisms. The decrease in microbial biomass was stronger in soil with high microbial activity compared with soil with low activity (Van Gestel *et al.*, 1993a).

Most of the released biomass C is attributed to the release of intracellular organic solutes into the environment, though not all bacteria seem to follow this strategy (Halverson *et al.*, 2000; Fierer & Schimel, 2003). The extracellular solute pool may consist of a variety of inorganic and organic compounds (e.g.  $K^+$ , carbohydrates, amino acids, amides, nucleotides) and may be used as energy source or reassimilated for microbial growth. Reassimilation of organic solutes would reduce the energetic costs for their production and allows rapid regrowth of microbial biomass. In a study by Bottner (1985), microbial biomass rapidly recovered in a wetted soil to the same size as the permanently moist soil. An increase in microbial biomass C after rewetting was also observed by Lundquist *et al.* (1999) for agricultural soils.

The release of microbial substrates during wetting seems to be one important C and N source in many but not all soils. Its contribution to the wetting pulse will depend on the change in water potential during drying and wetting and on the recycling of compatible solutes for microbial growth. Quick response and recovery of microbial activity and biomass after wetting suggests that most microbial communities are well-adapted to both drying and wetting stress even when a portion of the microbial population is killed during these extreme events. The situation might be different in soils or soil horizons that do not regularly experience drying/wetting cycles (Lundquist *et al.*, 1999). Such disturbances could sustainably reduce the population of slow-growing microorganisms and inhibit related processes such as autotrophic nitrification.

#### Availability of nonmicrobial substrates

Some studies showed that the mineralization of microbial C and N after wetting is smaller than the mineralization of nonmicrobial substrates. The availability of both sources for C and N mineralization is generally correlated with the organic matter content (Van Gestel *et al.*, 1993b; Franzluebbers *et al.*, 2000; Gordon *et al.*, 2008). For example, Van Gestel *et al.* (1991) explained most of the wetting pulse of pasture soils by mineralization of nonmicrobial substrates. In a grassland soil subjected to five dry-wet cycles, about 60% of the  $CO_2$  production originated from organic matter (Wu & Brookes, 2005). Appel (1998) concluded that microbially available organic N of dried-wetted arable soils mainly originated from the same nonmicrobial biomass N pool as in undried soil, suggesting that microorganisms were

not killed in these soils by drying or wetting. Microbial biomass C may not only be mineralized during wetting, but also enhance the mineralization of soil organic matter. Some microbially derived organic compounds have faster turnover times than plant material and additionally accelerate the decay of added plant material during drying and wetting of soils (Van Gestel *et al.*, 1993c). The pool of fresh litter (i.e. roots and leaves) accumulates during drought periods and becomes available for microorganisms following wetting.

The increased availability of nonmicrobial biomass substrates after wetting is mainly attributed to improved diffusive transport of organic and inorganic soluble substrates and regained mobility of microorganisms. If these were the only effective mechanisms, the adjustment of the water potential to control level would cause no wetting pulse or priming effect as illustrated in Fig. 1b. Such a scenario is likely under mild drying and wetting conditions when no other sources are accessible for C and N mineralization.

Nonmicrobial substrates may also become available during drying and wetting due to disruption of soil macroaggregates, desorption and exposure of organic matter on previously protected soil surfaces. Repeated drying and wetting reduced the amount of large macroaggregates (>2 mm) and the proportion of microaggregates within macroaggregates while the amount of free microaggregates increased during the first two dry-wet cycles (Denef *et al.*, 2001a,b). The release of microaggregates as well as the disruption of macroaggregates increase the accessibility of organic matter for microbial attack. In the following drying/wetting cycles, macroaggregates became slake-resistant and showed similar aggregate turnover as the permanently moist control, suggesting that the effect of this physical disturbance on the availability of soil organic matter and thus on microbial activity is limited to a few dry-wet cycles (Denef *et al.*, 2001a,b).

Disturbance of the aggregate structure by sieving or homogenization as reported for most laboratory studies (Tables 1 and 2) could have artificially increased the availability of nonmicrobial biomass substrates and microbial activity. Because soil texture has a direct effect on the number, size, formation, and stability of soil aggregates, fine-textured soils may have a larger potential of substrate release by physical disturbance than coarse-textured soils. Degens & Sparling (1995) described a sandy-loam soil that showed no increase in C mineralization subjected to repeated mild wet-dry cycles. Similarly, Jager & Bruins (1975) found no effect of drying and wetting on C mineralization in a sandy soil.

Overall, the influence of aggregate disruption on C and N mineralization is limited to rather few dry-wet cycles and tentatively restricted to clayey soils. One

possible explanation is the partly balanced formation and disruption of soil aggregates during drying and wetting. Moreover, water-repellent substances temporarily protect soil aggregates and embedded soil organic matter (Goebel *et al.*, 2005). In conclusion, C and N mineralization will increase during wetting with increasing pool of accessible C and N substrates (Table 3).

### *Hydrophobicity*

Hydrophobicity of soil organic matter considerably slows down the increase in water potential following wetting. After a drought period, most rainwater infiltrates along preferential flow paths into the soil or runs off at the soil surface in hilly and mountainous landscapes. The remoistening of topsoils often continues over weeks or months, depending on the hydrophobicity of the soil, initial water potential, and the intensity and duration of precipitation. Preferential flow hampers the overcoming of hydrophobicity because parts of soil organic matter have little or even no contact with water during rainfall. In a throughfall exclusion experiment in a temperate forest, the volumetric water content of the organic layer remained below the control level for about 3 months although 223 mm throughfall within 2.5 months should have completely rewetted the organic layer after the drought manipulation (Fig. 2). A slow increase in water potential gives microorganisms more time to equilibrate with their environment and to restore their metabolism including reassimilation of compatible solutes. Hence, the wetting of hydrophobic soil possibly means less stress for microorganisms as suggested by some authors (Halverson *et al.*, 2000; Schimel *et al.*, 2007).

The effects of soil hydrophobicity on C and N mineralization are barely investigated. Carbon mineralization of a farmland, grassland, and forest soil declined with increasing hydrophobicity (Goebel *et al.*, 2005, 2007). Addition of hydrophobic substances reduced the CO<sub>2</sub> losses of an agricultural soil by 30% (Piccolo *et al.*, 1999). These studies indicate that even weak hydrophobicity will reduce the mineralization of soil organic matter. We presume that hydrophobicity is likely to be an important mechanism that particularly diminishes C and N mineralization in organic soils and forest floors (Table 3). As C and N mineralization in many forest soils is located in the forest floor, these soils should be more affected by hydrophobicity than soils of grassland and farmland.

### **Quantifying the effect of drying and wetting: definition of the control**

The evaluation of drying and wetting effects on process rates often refers to a control soil that is kept

**Table 1** Effects of drying and wetting on cumulative C mineralization in soils from different land-use systems and geographical origins under laboratory conditions

Land use	Geographic, climatic information*	Soil	Soil treatment	Soil moisture	Incubation temperature (°C)	Drying period (days)	Wetting period (days)	Dry-wet cycles	Change in cumulative C mineralization	Reference
Arable land	Temperate; humid	Mineral soil	Sieved	Air-dried	29	3	28	60	0	1
	Temperate; subpolar; humid	Organic soils	Soil cores	Air-dried	RT†	21	7–9	2–3	0; +; +	2
	Subtropical; subhumid	Mineral soil	Sieved	–1.5 MPa	25	10	14	4	–	3
	Temperate; humid	Mineral soil	Homogenized	–3.8 MPa	14	9	91	1	–	4
	Temperate; humid	Mineral soils	Sieved, <sup>14</sup> C-labeled	–1180 MPa	25	3	10	1	+; +	5
	Temperate; semiarid	Mineral soil	Sieved, <sup>13</sup> C-labeled straw	0.01–0.02 g g <sup>–1</sup>	25	2	12	4	0	6
	Temperate; humid	Mineral soil	Sieved, <sup>14</sup> C-labeled	Air-dried	20	2	30	8–16	+	7
	Temperate; humid	Organic soils	Soil cores	Air-dried	RT†	21	7–9	2–3	+	2
	Temperate; subhumid	Mineral soil	Homogenized	Air-dried	28	8–10	15–20	4	+	8
	Temperate; humid	Mineral soil	Sieved	10% WHC	15	10	50	1	+	9
Grassland	Temperate; humid	Mineral soil	Sieved	Air-dried	25	1	7	5	+	10
	Subtropical; semiarid	Mineral soil	Sieved	Air-dried	4; 25	1; 6	1; 6	6	–; 0	11
	Subtropical; semiarid	Mineral soil	Sieved	–15 MPa	20	2	2–58	1–15	–	12
	Subtropical; semiarid	Mineral soil	Sieved	–30 MPa	20	3	6	1	+	13
	Subtropical; semiarid	Mineral soil	Sieved, <sup>14</sup> C glucose	Air-dried	25	10	4	3	–	14
	Subpolar; humid	Organic soil	Soil cores	Air-dried	RT	21	7–9	2–3	0	2
	Temperate; humid	Organic/ mineral soil	Soil cores	0.23; 0.53 g g <sup>–1</sup>	15	42	16–29	3	–	15
	Temperate; humid	Forest floor	Sieved	0.1 g g <sup>–1</sup>	20	12	13	1	–	16
	Subtropical; semiarid	Mineral soil	Sieved	–15 MPa	20	2	2–58	1–15	+	12
	Subtropical; semiarid	Mineral soil	Sieved	–30 MPa	20	3	6	1	+	13
Forest	Subpolar; humid	Litter	Litterbags	5% WHC	Field	6	1	4	–	17
	Subtropical; semiarid	Sandy clay loam	Sieved	–2.0 MPa, 4%	20	5–6	8–22	4–8	+	18
				WHC						

Increase (+), decrease (–) or no change (0) in cumulative C mineralization during drying and wetting relative to moist control or moist condition before drying.

\*Geographical zones: tropical, 0–20°; subtropical, 20–40°; temperate, 40–60°; subpolar, 60–70°, polar >70°. Humidity: arid, 10–12 months precipitation (P) < evapotranspiration (E); semiarid, 6–9 months P < E; subhumid, 6–9 months P > E; humid, 9–12 months P > E.

†RT, room temperature, not further defined.

References: 1, Jager & Bruins (1975); 2, Prieme & Christensen (2001); 3, Mikhla *et al.* (2005); 4, Magid *et al.* (1999); 5, Van Gestel *et al.* (1993a); 6, Denef *et al.* (2001a); 7, Sorensen (1974); 8, Bothner (1985); 9, Gordon *et al.* (2008); 10, Wu & Brookes (2005); 11, Degens & Sparling (1995); 12, Fierer & Schimel (2002); 13, Fierer & Schimel (2003); 14, van Veen *et al.* (1985); 15, Muhr *et al.* (2008); 16, Pulleman & Tietema (1999); 17, Schimel *et al.* (1999); 18, Miller *et al.* (2005).

**Table 2** Effect of drying and wetting on cumulative net N mineralization in soils from different land-use systems and geographical origins under laboratory conditions

Land use	Geographic, climatic information*	Soil	Soil treatment	Minimum soil moisture	Incubation temperature period (°C)	Drying period (days)	Wetting period (days)	Dry-wet cycles	net N mineralization	Method	Reference	Change in cumulative
												KCl extract
Arable land	Temperate; humid	Mineral soils	Sieved, inoculated	Oven-dried; air dried	70; 22	1	28	2	+			
	Subtropical; subhumid	Mineral soil	Sieved	-1.5 MPa	25	10	14	4	-	KCl extract	2	
	Subtropical; humid	Mineral soils	Sieved	0.003–0.007 g g <sup>-1</sup>	30	1	20	1	+	KCl extract	3	
	Temperate; humid	Mineral soil	Homogenized	-0.1; -1.5 MPa	25	1–4	21	1	+	KCl extract	4	
	Temperate; humid	Mineral soil	Sieved	Air-dried	25	<1	8·61	1	- to +	CaCl <sub>2</sub> extract	5	
	Subtropical-temperate; subhumid-humid	Different soils, n = 20	Sieved	Air-dried	25	10	10	1	- to +	KCl extract	6	
Grassland	Temperate; humid	Mineral soil	Sieved	10% WHC	15	10	50	1	+	Leaching	7	
	Temperate; humid	Forest floor	Soil cores	0.23 g g <sup>-1</sup>	15	42	16·29	3	-	Leaching	8	
	Temperate; humid	Mineral soil	Soil cores	0.53 g g <sup>-1</sup>	15	42	16·29	3	-	Leaching	8	
	Temperate; humid	Forest floor	Sieved	0.1 g g <sup>-1</sup>	20	12	13	1	-	KCl extract	9	
Chaparral	Subtropical; semiarid	Sandy clay loam	Sieved	-2.0 MPa, 4%	20	5–6	8·22	4; 8	0; +	K <sub>2</sub> SO <sub>4</sub> extract	10	
Rangeland	Tropical; semiarid	Mineral soil	Pot experiment	-0.42; -5.91 MPa	22	24	9	1	-	KCl extract	11	

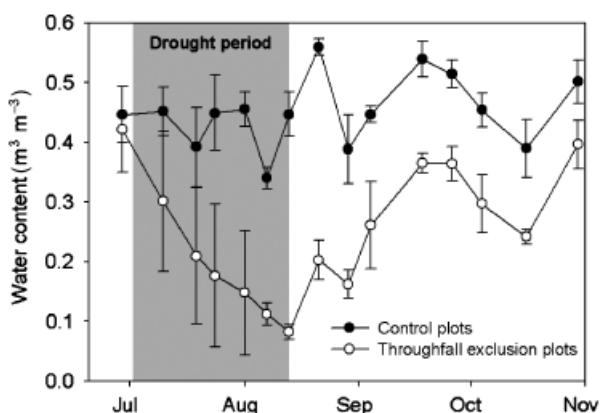
Increase (+), decrease (-) or no change (0) in cumulative net N mineralization during drying and wetting of soils relative to moist control or moist condition before drying.

\*Geographical zones: tropical, 0–20°; subtropical, 20–40°; temperate, 40–60°; subpolar, 60–70°, polar >70°. Humidity: arid, 10–12 months precipitation (P) < evapotranspiration (E); semiarid, 6–9 months P < E; subhumid, 6–9 months P > E; humid, 9–12 months P > E.

References: 1, Marumoto *et al.* (1982); 2, Milkha *et al.* (2005); 3, Cabrera (1993); 4, Seneviratne & Wild (1985); 5, Appel (1998); 6, Sparling & Ross (1988); 7, Gordon *et al.* (2008); 8, Hentschel *et al.* (2007); 9, Puleman & Tietema (1999); 10, Miller *et al.* (2005); 11, Pilbeam *et al.* (1993).

**Table 3** Potential influence of environmental factors and soil properties on cumulative C and net N mineralization following drying and wetting

Increase of	Cumulative C and net N mineralization
Drying period	Decrease
Wetting period	Increase
Drying intensity	Decrease
Wetting intensity	Increase
Drying and wetting frequency	Decrease
Accessible C and N pool	Increase
Hydrophobicity	Decrease



**Fig. 2** Mean volumetric water content ( $\pm$  SE) of the Oa horizon in control ( $n = 3$ ) and rainfall exclusions plots ( $n = 3$ ) of a Norway spruce stand at the Fichtelgebirge, Germany. Volumetric water contents were measured in each plot with 10 pseudo-replications using a transportable frequency domain reflectometry (FDR) probe (MI-2x, Delta-T Devices Ltd, Cambridge, UK).

permanently moist (laboratory studies) or variably moist (field studies) during drying/wetting cycles. The comparison between the control and treatment allows quantifying the net or priming effect of drying and wetting on C and N mineralization and other processes. Aside from the fact that the term 'permanently moist soil' is not well-defined, it does not necessarily imply that the optimum soil moisture for C and N mineralization is adjusted. When the moisture level of the control is at an optimum, the priming effect is relatively small (Fig. 1a), but the apparent priming effect will grow with decreasing moisture level in the control (Fig. 1c). Moreover, the water potential of wetted and control soil may differ due to hydrophobicity and hysteresis effects. All these uncertainties could interfere with the intrinsic priming effect and lead to misinterpretations. Adjustment of water potentials by changing the osmotic potential has overcome these hydrological difficulties (Halverson *et al.*, 2000), but

the sudden increase in osmotic potential by water addition has other disadvantages as discussed earlier.

The evaluation of natural or experimentally induced drying and wetting effects under field conditions is even more difficult. In rainfall exclusion experiments, the control soil is subjected to natural changes in soil moisture and often apart from optimum soil moisture conditions. An alternative to rainfall exclusion experiments is the permanent irrigation of the soil that allows the quantification of natural drought effects. Because a permanently moist treatment is generally not established in field experiments, the use of the term 'priming effect' is misleading in order to describe the increase in mineralization. Additionally, the priming effect refers to C and N mineralization in soils, but these process rates cannot be simply separated from root respiration and inorganic N uptake by roots.

#### Effects of intensity and duration of drying and wetting on cumulative C and N mineralization

Here, we define the intensity of soil drying as the minimum water potential usually reached directly before wetting. Correspondingly, the intensity of wetting is defined as the amount of precipitation or added water per day. Systematic studies on the effect of drying or wetting intensity on C and N mineralization are rare and a comparison of the study results (Tables 1 and 2) is difficult given different information on soil moisture.

Even small precipitation events may cause a short-term CO<sub>2</sub> pulse of few hours as reported for a variety of soils (Huxman *et al.*, 2004b; Lee *et al.*, 2004; Cisneros-Dozal *et al.*, 2007). The size of the wetting pulse increased with the amount of applied water, though CO<sub>2</sub> production quickly returned to background levels when the soils dried out (Borken *et al.*, 2003; Sponseller, 2007). No effects on cumulative fluxes of CO<sub>2</sub> and inorganic N were observed when equal amounts of water (100 mm) were distributed to dry soils with different intensities over 2–12.5 days (Hentschel *et al.*, 2007; Muhr *et al.*, 2008), indicating that precipitation pattern has no influence on small time scales. This laboratory result, however, cannot simply be transferred to field conditions. Heavy rainfall can lead to runoff or rapid infiltration, and thus reduced soil moisture compared to small and long-lasting precipitation. An extended wetting period and slow increase in soil respiration was generated in a field experiment by sprinkling small amounts of water (1–2 mm day<sup>-1</sup>) on the dry soil over several weeks (Borken *et al.*, 1999). This scenario might be rather typical in semiarid regions with extended dry and rainy seasons.

The duration of drying and wetting is of large importance for cumulative C and N mineralization. A relatively short drying period and extended wetting period as performed in many laboratory studies (Tables 1 and 2) would potentially result in greater cumulative C and N mineralization relative to a moist control (Fig. 1d). Moreover, the duration of drought influences the population of soil microorganisms during drying and wetting. A natural 2-week drought and occasional precipitation reduced C mineralization of birch litter to a greater extent as compared with repeated short-term dry-wet cycles (Schimel *et al.*, 1999). They concluded that the reduction in microbial activity resulted from a time-dependent decrease in microbial populations. In another field experiment, air-dried aspen and alder litter decayed much slower than respective fresh-fallen litter and remained drier throughout the entire year (Taylor, 1998). A similar result was obtained when organic horizons from a spruce forest were subjected to three dry-wet cycles (Hentschel *et al.*, 2007). The water content of the desiccated soil remained below the permanently moist control and caused, at least in part, a reduction of N fluxes.

These results suggest that the duration as well as the intensity of drying may affect C and N mineralization during the wetting and postwetting period. The conditions during wetting cannot be considered as independent parameters and thus more holistic studies are needed to improve our understanding. In general, cumulative mineralization rates theoretically decrease with increasing duration and intensity of desiccation (Table 3). Rainfall intensity has only a limited effect on C and N mineralization while the duration of the wetting period will influence the cumulative mineralization rates.

#### **Effect of drying and wetting frequencies on cumulative C and N mineralization**

Changes in soil moisture regularly occur in ecosystems and are considered together with temperature as the main drivers of the mineralization processes. Drying of the soil surface starts shortly after the last rain event by evaporation and slowly proceeds in the rooting zone by transpiration until the next rain event. In many climatic regions, topsoils are consequently subjected to frequent dry-wet cycles, whereas the underlying soil is less often influenced by rapid changes in soil moisture. The gradient in soil moisture is of relevance for the overall mineralization considering that litter with high mineralization potential is mostly accumulated in topsoils. Exceptions are Mediterranean, semiarid, arid, and some tropical regions where precipitation is unevenly distributed throughout the year. Here, underlying soils may

experience similar and severe dry-wet frequency as topsoils.

The analysis of literature (Tables 1 and 2) revealed a fairly consistent picture. The size of wetting pulses decreases with the frequency of dry-wet cycles (Table 3). This has been shown for soils from farmland (Jager & Bruins, 1975; Prieme & Christensen, 2001; Mikha *et al.*, 2005), grassland (Fierer & Schimel, 2002), and forest (Fierer & Schimel, 2002). The decrease in wetting pulse may be explained by the decrease in labile organic matter over time (Birch, 1958a) or by a shift in bacterial community composition as reported for a forest soil (Fierer *et al.*, 2003). In the latter study, repeated drying and wetting did not affect the bacterial community in the grassland soil, indicating that bacteria were adapted to this stress.

#### **Relevance of drying/wetting cycles for cumulative C and N mineralization and fluxes**

Mineralization or flux rates obtained from laboratory studies cannot be transferred to the ecosystem scale, but may give a hint of the direction in which the soils will respond to drying and wetting. As pointed out above, the definition of a control soil is a useful tool for the evaluation of drying and wetting effects. Under laboratory condition, the control soil is often in the optimum moisture range (see references cited in Tables 1 and 2), but this is unrealistic under field conditions over a longer period. In the field, the control soil will vary in its moisture level with natural weather conditions, which could result in opposing effects of drying and wetting between the years.

#### *Cumulative C mineralization and CO<sub>2</sub> fluxes*

Laboratory studies on soils from arable land, grassland, forest, and other systems indicate no systematic difference in cumulative C mineralization after drying and wetting (Table 1). About 50% of these studies revealed an increase in cumulative C mineralization following drying and wetting, whereas the other studies showed no change or decrease in cumulative C mineralization relative to a moist control soil. It seems that the results were partly affected by the duration of the drying and wetting periods as, for example, illustrated in Fig. 1d. In about one-third of these studies, the drying period was longer than the wetting period, mostly resulting in a decreasing or unaffected cumulative C mineralization rate. Only Prieme & Christensen (2001) reported increasing cumulative C mineralization rates in organic soils at relatively long drying periods.

In some laboratory studies with longer wetting than drying periods (Table 1), the total effect on cumulative

C mineralization is probably overestimated, when extrapolated to field conditions. The evaluation of C mineralization rates during wetting periods, however, is difficult because soil moisture is in some studies constant or decreases in other studies after wetting. Considering the temperature range of 4–35 °C together with other experimental differences (Table 1), the magnitude of the flush following the wetting of dry soil, as well as cumulative C mineralization rate is largely experiment-specific and does not allow the extrapolation to annual C fluxes under field conditions.

In field experiments, the simulation of less precipitation or prolonged drought periods revealed a reduction or no change in annual CO<sub>2</sub> efflux (Table 4). An exceptional increase in annual CO<sub>2</sub> efflux of 1.7 Mg C ha<sup>-1</sup> yr<sup>-1</sup> was observed only when the drought plot was artificially irrigated during a warm period while the control soil remained dry (Borken *et al.*, 1999). The annual CO<sub>2</sub> efflux was not affected at this site when the soil was irrigated in September/October. This shows that the pattern in precipitation and the temperature during wetting may have a great impact on annual CO<sub>2</sub> efflux as the control as well as the drought plot received the same amount of throughfall.

Surprisingly, no effect on annual CO<sub>2</sub> efflux was found by throughfall reduction in a temperate forest (Hanson *et al.*, 2003) and a tropical rain forest (Davidson *et al.*, 2004). Even the increase in throughfall by 33%

achieved no change in annual CO<sub>2</sub> efflux (Hanson *et al.*, 2003). In contrast, Sotta *et al.* (2007) found a decrease in annual CO<sub>2</sub> efflux by 26% in a tropical rain forest, although the reduction in throughfall was weaker (50%) as compared with the site (72–75%) of Davidson *et al.* (2004). The different response was explained by the differences in the stock of plant available water (PAW) (Sotta *et al.*, 2007) that is controlled by soil texture, organic matter content, soil, and rooting depth. The results suggest that the reduction in throughfall during natural precipitation events has only an effect on annual CO<sub>2</sub> efflux if the stock of PAW is significantly reduced.

Significant transient C losses following the wetting of dry soils were reported from Mediterranean ecosystems (Reichstein *et al.*, 2002; Xu *et al.*, 2004; Jarvis *et al.*, 2007). These ecosystems turned into a net C source due to immediate increases in soil CO<sub>2</sub> effluxes with incipient precipitation in summer or autumn. Xu *et al.* (2004) postulated the mineralization of surplus organic matter during wetting as the CO<sub>2</sub> pulse could not be explained by a moisture–temperature dependent function. CO<sub>2</sub> uptake by plants responded with a delay to the rainfall events, but exceeded C mineralization most days of the year, resulting in an annual net C sink of the ecosystem. One may argue that soil C losses would increase with increasing frequency of rain events during dry summers as long as plant productivity is not affected by elevated water availability.

**Table 4** Effects of summer throughfall exclusion, experimental or natural wetting on soil CO<sub>2</sub> fluxes under field conditions

Ecosystem	Length of throughfall exclusion	Reduction in annual throughfall/rainfall	Wetting period	Amount of water during wetting (mm)	Annual precipitation (mm)	Change in CO <sub>2</sub> efflux	Reference
Tropical rainforest	3 years, not during dry season	72–75%	–	–	600–3000	No change	Davidson <i>et al.</i> (2004)
Tropical rainforest	2 years, partly during dry season	50%	–	–	2272	–26%	Sotta <i>et al.</i> (2007)
Temperate forest	–	–	Storm event, 26 h	170	1330	0.18 Mg C ha <sup>-1</sup> yr <sup>-1</sup>	Lee <i>et al.</i> (2004)
Temperate spruce forest	170; 108 days	483; 250 mm	19; 32 days	193; 184	1090	–0.03; 1.7 Mg C ha <sup>-1</sup> yr <sup>-1</sup>	Borken <i>et al.</i> (1999)
Temperate mixed forest	84; 127 days	168; 344 mm	–	–	1050	–1.1; –2.1 Mg C ha <sup>-1</sup> yr <sup>-1</sup>	Borken <i>et al.</i> (2006)
Temperate mixed forest	8 years	33%	–	–	1329	No change	Hanson <i>et al.</i> (2003)
Temperate mixed forest	–	–	8 years	33% of TF	1329	No change	Hanson <i>et al.</i> (2003)
Different shrublands ( <i>n</i> = 4)	55–244 days	9–82%	–	–	455, 758; 1042–1741	–3% to –29%	Emmett <i>et al.</i> (2004)

TF, throughfall.

Temperate and boreal ecosystems are less subjected to severe drought periods and subsequent wetting, though future changes in precipitation may have an outstanding effect on the large soil organic C stock in these regions. Lee *et al.* (2004) found a soil CO<sub>2</sub> flush of 0.2 Mg C ha<sup>-1</sup> equivalent to 5–10% of net ecosystem exchange (NEE) caused by a single storm event. A boreal aspen forest exhibited very high annual NEE as a result of elevated photosynthetic CO<sub>2</sub> uptake during early spring and reduced soil respiration in the topsoil during a summer drought (Kljun *et al.*, 2006). Soil moisture in deeper soil horizons decreased much slower and allowed the trees to maintain water uptake over an extended period. In drier years, however, NEE was considerably lower due to the decrease in photosynthetic CO<sub>2</sub> uptake. It appears that the amount of PAW as well as the vertical root distribution is an important key factor for the response of soil respiration to drying and wetting.

Soil respiration includes the contribution of root-associated respiration and decay of soil organic matter. Drying and wetting may differently affect the activity of roots and microbes, indicating that the changes in soil respiration cannot be attributed to the one or the other component. The analysis of <sup>14</sup>CO<sub>2</sub> allowed the partitioning of soil respiration in a throughfall exclusion experiment without any disturbances (Borken *et al.*, 2006). In this study, the decay of soil organic matter was more strongly reduced by soil drought than by root respiration. The accumulated organic matter (approximately 1.9 Mg C ha<sup>-1</sup> in two consecutive years) was only partly mineralized during the following year of natural rainfall. We postulated that the soil may become at least a transient C sink during extended drought periods and that rain events will reduce the sink strength. In another study using radiocarbon signatures of respired CO<sub>2</sub>, the decomposition of the litter layer was strongly subjected to frequent drying and wetting and its contribution to soil respiration may increase from 5% to 37% after water addition and vice versa (Cisneros-Dozal *et al.*, 2007).

The results indicate that C mineralization under field conditions is often limited during the growing season by moisture deficit in the organic layer or top mineral soil. In boreal and temperate forests, the moisture deficit together with suboptimal temperatures may have contributed to the accumulation of thick organic horizons. Kelliher *et al.* (2004) predicted a 2.5-fold increase in annual soil respiration for a semiarid pine forest in a hypothetically wet year without any water limitation. Such dramatic changes may not be expected in temperate and boreal zones, but cumulative C mineralization would probably increase with increasing frequency of rain events (i.e. more small rainfall events as compared

to few large rainfall events) during the growing season (Table 3).

#### Cumulative net N mineralization and N fluxes

Similar to the laboratory results on cumulative C mineralization, drying and wetting has dissenting effects on net N mineralization and fluxes in soils from different land-use systems (Table 2). The differences may be partly explained by the duration of drying and wetting periods and the treatment of soils. Extreme desiccation within a short period followed by an extended wetting period is a nonrealistic scenario for most ecosystems. With one exception, all studies with increased cumulative net N mineralization experienced longer wetting than drying periods. Only Sparling & Ross (1988) reported an increase in cumulative net N mineralization in 18 of 20 grassland soils at equal lengths of the drying and wetting periods. The amount of extracted N was positively correlated with the total N content of the dried and wetted soils. It seems that cumulative net N mineralization is more sensitive to the frequency of drying and wetting than cumulative C mineralization. In a laboratory experiment, repeated 4-week drying/wetting cycles reduced net N mineralization more strongly compared with 2-week drying/wetting cycles while C mineralization was not affected by the frequency of drying/wetting cycles (Miller *et al.*, 2005).

The observed changes of inorganic N concentrations are mainly the result of gross rates of ammonification and nitrification, biotic and abiotic immobilizations, and denitrification. To our knowledge, the response of gross and net rates of ammonification and nitrification to drying and wetting has been barely studied. In one of the few studies, wetting of dry soil from a semi-arid ecosystem initially stimulated gross N mineralization to a greater extent than N immobilization, causing a short-lived wetting pulse of inorganic N (Saetre & Stark, 2005). After a few days, however, both gross N mineralization and immobilization decreased to similar rates. Breuer *et al.* (2002) reported decreasing gross nitrification rates with stepwise addition of water, but concomitant increasing emissions of N<sub>2</sub>O in two tropical forest soils. A third tropical soil exhibited increasing gross nitrification rates but released almost no N<sub>2</sub>O. Other studies revealed large gaseous fluxes of NO and N<sub>2</sub>O in wetted soils (Sexstone *et al.*, 1985, 1988; Davidson, 1992; Davidson *et al.*, 1993; Prieme & Christensen, 2001), indicating that a fraction of mineralized N can be lost via nitrification and denitrification during wetting. However, these short-term wetting pulses cannot compensate for the decrease in gaseous losses during extended drought periods. For example, Davidson *et al.* (2004) found about 40% reduced N<sub>2</sub>O emissions

through a partial exclusion of rainfall in a tropical rainforest.

Despite the diverse processes and pathways of the microbial N cycle, net N mineralization provides some useful information about potential N availability for plants or the risk of N leaching. N losses by leaching following drying and wetting of soils depend on the N uptake by plants and the water flux in the soil. In arid and semiarid regions, the risk of N leaching is negligible due to small water fluxes, and so inorganic N may accumulate in the soil or be immobilized either by microorganisms or plants. The nitrate pulse was short-lived in a semiarid steppe probably because of rapid microbial immobilization after water addition (Cui & Caldwell, 1997). A study in a similar ecosystem suggests that the wetting intensity has no effect on *in situ* net N mineralization on an annual scale (Yahdjian *et al.*, 2006). Ecosystems with small organic N stock and N turnover seem to have a limited risk of N leaching owing to drying and wetting. Heavy rainstorms could potentially cause small leaching or runoff losses of inorganic N. In contrast, annual rates of net N mineralization or nitrate leaching decrease with the increasing duration of drought (Emmett *et al.*, 2004). The reduction in N leaching can be large in N-saturated ecosystems as reported for a spruce forest subjected to experimental summer drought and subsequent wetting (Xu *et al.*, 1998). In two consecutive years, about 5 and 11 kg N ha<sup>-1</sup> yr<sup>-1</sup> less were leached below the rooting zone. A decrease in net N mineralization of 60–70% was observed in a microplot field study on farmland (Bloem *et al.*, 1992). The dried and subsequently wetted soils never reached the level of the moist control within the wetting period of 11 days.

In agreement with the rainfall exclusion studies (Table 5), irrigation enlarged N leaching losses of coniferous soils by 11.5 and 14.2 kg N ha<sup>-1</sup> yr<sup>-1</sup> (De Visser, 1995; De Visser & van Breemen, 1995). Matson *et al.* (1992) reported deviant net N mineralization rates for an irrigated mountainous Douglas-fir forest. The annual *in situ* net N mineralization rate was reduced in the forest floor and enhanced in the mineral soil of the irrigated plots, though the reason for the different responses is not known.

In spite of the contradictory laboratory results, the field studies predominantly indicate decreasing net N mineralization and inorganic N fluxes with increasing duration and intensity of drought periods (Table 3). The net N mineralization pulses following the wetting of dry soils appear to be relatively small or insignificant on an annual scale. Increasing precipitation during the growing season will likely enhance the leaching losses of inorganic N in N-rich ecosystems (Table 3).

**Table 5** Effects of summer throughfall exclusion, wetting experiments or natural wettings on net N mineralization or fluxes under field conditions

Ecosystem	Length of throughfall exclusion	Reduction in annual throughfall/rainfall	Irrigation period	Amount of water during wetting (mm)	Annual precipitation (mm)	Change in N mineralization/ N fluxes	References
Arable farmland, microplot experiment	32 days	nd (from -0.03 to -0.12 MPa)	10 days	nd, wetted to -0.03 MPa	650–800	-60% to -70%	Bloem <i>et al.</i> (1992)
Mountainous fir forest	–	–	June–September	40 per week	~2100	-27.6 (forest floor), 7.4 µg N g <sup>-1</sup> yr <sup>-1</sup> (mineral soil)	Matson <i>et al.</i> (1992)
Semiarid steppe	2 years	30%, 55% and 80%	–	–	168	No effect	Yahdjian <i>et al.</i> (2006)
Temperate spruce forest	170; 108 days	483; 250 mm	19; 32 days	193; 184	1090	-4.8; -10.8 kg N ha <sup>-1</sup> yr <sup>-1</sup>	Xu <i>et al.</i> (1998)
Temperate Douglas fir stand	–	–	Growing season	6–8 every second day	853	14.2 kg N ha <sup>-1</sup> yr <sup>-1</sup>	De Visser (1995)
Temperate Scots pine stand	–	–	Growing season	6–8 every second day	760	11.5 kg N ha <sup>-1</sup> yr <sup>-1</sup>	De Visser & van Breemen (1995)
Shrublands ( <i>n</i> = 4)	55–244 days	9–82%	–	–	455, 758; 1042–1741	No change or small decrease	Emmett <i>et al.</i> (2004)

## Conclusions

The mechanisms that induce changes in C and N mineralization by drying and wetting have been largely identified in numerous laboratory studies. A clear deficit, however, exists on the effect of soil hydrophobicity on microbial activity in soils with large organic matter contents. Under laboratory conditions, soils exhibit large differences in C and N mineralization following drying and wetting. These large variations may be explained by differences in experimental design (i.e. incubation temperature, duration, intensity and frequency of drying and wetting, treatment and properties of soils). Only few soils showed greater cumulative C and N mineralization rates following drying and wetting than the respective moist soils at similar durations of drying and wetting periods. Some evidence is given that specific soil microorganisms are better adapted to drying and wetting stress than others, but process rates are not inevitably affected by changes in microbial community structure. Further research is required to elucidate possible long-term shifts in microbial diversity. Net N mineralization is apparently more sensitive to drying and wetting than C mineralization. The fate of ammonium and nitrate, however, is not well known because of the variety of processes involved in N cycling. Estimates of gross turnover rates of ammonification and nitrification during both drying and wetting would provide valuable information.

Laboratory studies cannot be simply transferred to the ecosystem level due to the combination of different and possibly interacting mechanisms. Carbon and N mineralization and fluxes may differ under field conditions from laboratory studies through the influence of plants (water and nutrient uptake, root production, exudation), inhomogeneous patterns of soil moisture, soil aggregation, and different temperature regimes. Additionally, the design of field experiments and natural variations in weather conditions have a strong impact on the results. Despite these limitations, the present literature suggests that prolonged summer droughts and subsequent wetting will reduce cumulative soil C and N mineralization in all ecosystems on the annual scale. In contrast to the present understanding, relatively short wetting pulses can generally not compensate for low mineralization rates during the drought periods. Reversely, frequent precipitation and elevated soil moisture during growing seasons will promote the decay of soil organic matter. Thus, we suggest simultaneous rainfall exclusion and irrigation plots to overcome problems with interannual variations in precipitation in field experiments. Irrigation plots would allow accessing the limitations resulting from natural drought periods at ambient temperatures. Finally,

changes in soil C and N stocks are a question of how plant productivity, litter production, and mineralization will respond to changing precipitation and temperature regimes.

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