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Water pulses and biogeochemical cycles in arid and semiarid ecosystems

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Abstract The episodic nature of water availability in arid and semiarid ecosystems has significant consequences on belowground carbon and nutrient cycling. Pulsed water events directly control belowground processes through soil wet-dry cycles. Rapid soil microbial response to incident moisture availability often results in almost instantaneous C and N mineralization, followed by shifts in C/N of microbially available substrate, and an offset in the balance between nutrient immobilization and mineralization. Nitrogen inputs from biological soil crusts are also highly sensitive to pulsed rain events, and nitrogen losses, particularly gaseous losses due to denitrification and nitrate leaching, are tightly linked to pulses of water

availability. The magnitude of the effect of water pulses on carbon and nutrient pools, however, depends on the distribution of resource availability and soil organisms, both of which are strongly affected by the spatial and temporal heterogeneity of vegetation cover, topographic position and soil texture. The ‘inverse texture hypothesis’ for net primary production in water-limited ecosystems suggests that coarse-textured soils have higher NPP than fine-textured soils in very arid zones due to reduced evaporative losses, while NPP is greater in fine-textured soils in higher rainfall ecosystems due to increased water-holding capacity. With respect to belowground processes, fine-textured soils tend to have higher water-holding capacity and labile C and N pools than coarse-textured soils, and often show a much greater flush of N mineralization. The result of the interaction of texture and pulsed rainfall events suggests a corollary hypothesis for nutrient turnover in arid and semiarid ecosystems with a linear increase of N mineralization in coarse-textured soils, but a saturating response for fine-textured soils due to the importance of soil C and N pools. Seasonal distribution of water pulses can lead to the accumulation of mineral N in the dry season, decoupling resource supply and microbial and plant demand, and resulting in increased losses via other pathways and reduction in overall soil nutrient pools. The asynchrony of resource availability, particularly nitrogen versus water due to pulsed water events, may be central to understanding the consequences for ecosystem nutrient retention and long-term effects on carbon and nutrient pools. Finally, global change effects due to changes in the nature and size of pulsed water events and increased asynchrony of water availability and growing season will likely have impacts on biogeochemical cycling in water-limited ecosystems.

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Introduction

Although 30 years have passed since Noy-Meir (1973, 1974) highlighted how pulsed water events affect most aspects of ecosystem functioning in deserts, many questions remain regarding the importance of water pulses for controlling biogeochemical cycling in water-limited ecosystems. Episodic water availability clearly affects element cycling in arid and semiarid ecosystems (Schimel and Parton 1986; Gebauer and Ehleringer 2000), but to date, information on the quantitative effects of water pulses on belowground processes is relatively scarce. In part, the ephemeral nature of the effect of pulses on nutrient fluxes, such as gaseous losses due to ammonia volatilization during a small rain event (Schlesinger and Peterjohn 1991), or the instantaneous response of soil organisms to changes in moisture (Freckman et al. 1987; Schwinning and Sala 2004) contribute to the difficulty in obtaining reliable information on the effects of water pulses on ecosystem functioning. Moreover, essential to our understanding of how pulses affect belowground processes is the need to identify how water pulses interact with intrinsic spatial and temporal heterogeneity of carbon and nutrient pools, the differential effects of water pulses on soil biota, and the impact of water pulses on the balance between resource inputs and outputs in both space and time.

In ecosystems that receive less than 600 mm mean annual precipitation, primary production is thought to be largely constrained by water availability (Noy-Meir 1973; Lieth 1975; Webb et al. 1978; Sala et al. 1988), which is, in part, controlled by the nature and timing of rainfall events. At the same time, variation in precipitation input affects most other ecosystem processes as well. The frequency and periodicity of water pulses and their control on ecosystem processes can be examined at a number of scales (Schwinning and Sala 2004), including the timing and size of small rainfall events within a season (Sala and Lauenroth 1982), the seasonal distribution of rainfall (Frith and Frith 1990; Amundson et al. 1994; Reynolds et al. 1999; Jobbágy and Sala 2000), or the inter-annual variability in precipitation (Lauenroth and Sala 1992).

The objective of this review is to examine how water pulses affect biogeochemical cycles in arid and semiarid ecosystems, and to evaluate the importance of pulsed water events as a control on belowground processes. For the purposes of this review, we have chosen to focus on the shorter-time scale of pulsed rain events, examining how this variation in water availability affects biogeochemical cycling. In addition, we will explore our current gaps in knowledge, future directions of research, and the potential interaction with human-induced global change.

Water pulses in arid and semiarid ecosystems

The episodic nature of water input in arid and semiarid ecosystems has direct consequences on most ecosystem processes, and indirect consequences through its interac-

tion with other ecosystem characteristics. For example, water pulses may directly affect the frequency and duration of 'wet-dry cycles' in the soil, but these wet-dry cycles may indirectly control activity of soil organisms, which will ultimately determine carbon and nitrogen turnover. In addition, the effect of pulses of water on different ecosystem compartments may not be equal. Cryptobiotic organisms at the soil surface can often respond to small but relatively frequent rainfall events that wet only the top layer of soil when plants cannot, leading to a pulse after pulse phenomenon, whereby nitrogen availability may increase at a moment when plants are not able to capitalize on the available resource (Singh et al. 1989). This asynchrony of resource availability due to the nature of pulsed water events may be central to understanding the consequences for ecosystem nutrient retention and long-term effects on carbon and nutrient pools.

The spatial and temporal heterogeneity of resources and soil biota, however, must be considered in order to understand the effects of water pulses on biogeochemical cycles. The distribution of soil resources is heterogeneous because of the patchy distribution of vegetation, resulting in the well-documented "islands of fertility" and a discontinuous distribution of both water and nutrient resources (Charley and West 1975; Barth and Klemmedson 1978; Virginia and Jarrell 1983; Jackson and Caldwell 1993; Halvorson et al. 1994; Schlesinger et al. 1996; Zaady et al. 1996a; Aguiar and Sala 1999). Soil physical characteristics including differences in soil texture and porosity also contribute to differences in water infiltration rates and rainfall redistribution and surface runoff (Laio et al. 2001). Furthermore, the variable nature of life forms present in arid landscapes (i.e. shrubs, clumps of grass, bare and crusted interspaces) results in spatial heterogeneity of C and N pools. For example, protection from erosion by wind and water under shrubs, and higher vegetative cover results in increased inputs of carbon and nutrients (Vinton and Burke 1995), and the rate of cycling can change with life form or species (Chen and Stark 2000).

Due to this discontinuous vegetative cover, soil biota primarily occurs in vegetated patches (Santos et al. 1978; Whitford and Sobhy 1999; Belnap and Phillips 2001), and the distribution of microbial biomass is also heterogeneous, with higher concentrations of microbial populations and increased activity in vegetated patches than in bare soil (Gallardo and Schlesinger 1992; Bolton et al. 1993; López et al. 2003). This spatial discontinuity of microbial biomass and organic matter results in large differences in biogenic trace gas emissions, which are often heavily concentrated in shrub patches (Bolton et al. 1990; Bolton et al. 1993). In addition to heterogeneity in spatial distribution, soil fauna differ in their responses to soil drying and water pulses due to differences in desiccation resistance, drought avoidance and other short-term physiological changes (Kieft et al. 1987; Van Gestel et al. 1993; Mamilov and Dilly 2002), suggesting that the pulsed water availability could serve as a selective mechanism in arid and semiarid ecosystems for organisms with higher

resistance to wet-dry oscillations (Schwinning and Sala 2004). For example, protozoan activity is limited to periods when soil moisture is relatively high (>0.1 MPa) and movement is not limited by thin water films (Griffin 1981; Papendick and Campbell 1981). At the same time, nematodes and microarthropods are more tolerant of dry conditions, and do not always show a clear response to wetting events (Whitford et al. 1981).

Soil wet-dry cycles and carbon and nutrient dynamics

One of the principal consequences of the stochastic nature of water pulse inputs in arid and semiarid ecosystems is that surface soils experience periods of drying followed by relatively rapid rewetting. Drying-rewetting cycles are often most pronounced in arid and semiarid ecosystems with a strongly seasonal precipitation, but wet-dry cycles commonly occur in a variety of ecosystems (Kieft et al. 1987; Groffman and Tiedje 1988; García-Méndez et al. 1991; Mummey et al. 1994; Cui and Caldwell 1997; Ryan et al. 1998; Pulleman and Tietema 1999). As with precipitation events, wet-dry cycles can occur on different temporal scales. In highly seasonal ecosystems, such as tropical deciduous forests, one or two wet-dry cycles can take place within a year with each period lasting between four to six months (García-Méndez et al. 1991; Davidson et al. 1993; Jaramillo and Sanford 1995). Soil wet-dry cycles can occur at much faster intervals, however, encompassing days or even hours between sparse rain events (Sala and Lauenroth 1982; Whitford et al. 1986).

The effects of drying and rewetting cycles on biogeochemical processes have been studied in both agricultural and natural systems. These wet-dry cycles affect all aspects of carbon and nutrient turnover, including C and N mineralization (e.g. Birch 1964; Agarwal et al. 1979; Seneviratne and Wild 1985; Degens and Sparling 1995), microbial biomass (Bottner 1985; Kieft et al. 1987; Van Gestel et al. 1993), gaseous losses (Davidson et al. 1993; Mummey et al. 1994; Smart et al. 1999; Stark et al. 2002), denitrification (Groffman and Tiedje 1988; Peterjohn and Schlesinger 1991), and ammonia volatilization (Schlesinger and Peterjohn 1991; Heckathorn and Delucia 1995). A summary of changes in ecosystem processes and carbon and nitrogen pools when a pulsed water event occurs is shown in Fig. 1, which includes increased fluxes of C and N, changes in pool sizes of inorganic N and increased losses of C and N occur as a dry soil becomes wetted.

We present a summary of studies relating the effects of wet-dry cycles on soil C and N dynamics both under laboratory conditions (Table 1) and in field studies (Table 2) for soils from arid and semiarid ecosystems. What is most evident from both tables is that for soils that have not received recent organic matter additions, wet-dry cycles initially stimulate C and net N mineralization (usually within the first few hours for C mineralization), diminish microbial biomass during drying but stimulate microbial growth after wetting, and the wet-dry cycle itself

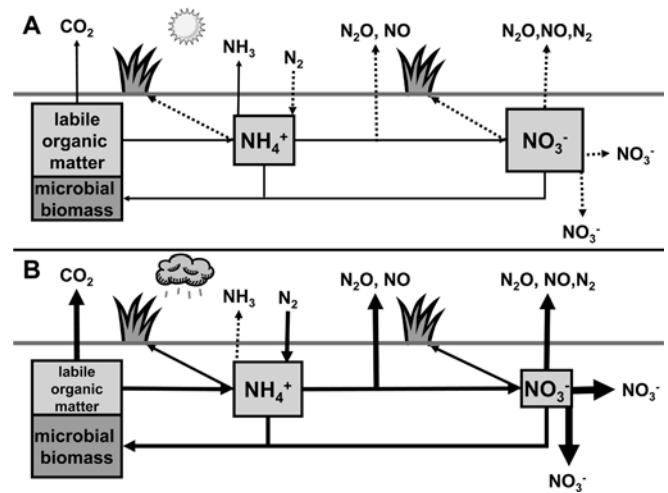


Fig. 1 Schematic outline of biogeochemical cycles of C and N in arid and semiarid ecosystems under **A** dry conditions, and **B** after a rainfall pulse. *Width of arrows* indicates the relative importance of these processes in the two situations. *Dotted lines* indicate that flows are either very low or undetectable. During interpulse periods, turnover of both C and N slows, microbial death occurs, and plant uptake is restricted, leading to an increase in soil NO₃⁻ and labile organic matter. When soils are wetted, stimulation of C and N mineralization and large changes in the relationship of soil microbial biomass and labile organic matter pools are commonly observed, and the potential for loss of labile N increases due to increased nitrification, denitrification and leaching

results in higher net N and C mineralization when compared to continuously moist soils. We found one exception to this pattern of increased C and N mineralization, where Degens and Sparling (1995) found no increase in organic C mineralization in a sandy loam soil subjected to six wet-dry cycles.

Both wet and dry phases have effects on soil processes, but it is the cyclical dynamic that determines the particular responses when compared to constant moisture conditions. For example, accumulation of inorganic N usually occurs during dry periods because diffusion of ions is severely restricted in thin water films of dry soil and because sinks of inorganic N are limited by reduced microbial growth and limited plant uptake (Barber 1995; Stark and Firestone 1995). In addition, a portion of the microbial biomass is killed under dry conditions (Bottner 1985), which is readily decomposed by surviving organisms when the soil is rewetted. Rapid change in soil water potential associated with rewetting may cause microbes to undergo osmotic shock, including microbial cell lysis (Bottner 1985; Van Gestel et al. 1993) or a release of intracellular solutes (Halverson et al. 2000). When dry soil is rewetted, diffusion is no longer restricted and the accumulated labile soil organic matter (SOM) and dead microbial biomass, with their low C:N ratios, become available for microbial activity. The availability of low C:N substrates, along with favorable conditions for microbial growth, lead to high gross and net N mineralization, large pulses of CO₂ and gaseous fluxes of N, and a pulse of increased C and N availability (Kieft et al. 1987; Peterjohn and Schlesinger 1991; Mummey et al. 1994). Alternatively, drying-

Table 1 Consequences of wet-dry cycles (WDCs) on net N and C mineralization measured under laboratory conditions. Increased or decreased response is shown relative to control conditions, in which soil moisture conditions were kept constant

Substrate type	C/N ratio	%C	No. of WDCs	Incubation period (days)	Net N mineralization	C mineralization	Microbial biomass	Reference
Soil	12.8	7.7%	1–3	30	↑ (8.3%) with successive WDCs	-	-	a
Sandy loam	10.6–11.4	1.6–2.0%	1	20	↑ with soil %N	-	-	b
Soil + grasses ^o	12–38	0.4%	1–3	21, 27, and 33	↑ with the number of WDCs, with time and with low C/N ratio of litter	-	-	c
Silt loam	11.1	2.1%	1	1	↑ NO flux (nitrification) (500%) within minutes of adding water	-	-	d
Soil	10.3	6.2%	2–3	50	-	↑ in the first hours after rewetting, then ↓ rapidly	-	a
Gravelly loam	-	3.3%	1	10	-	Flush of CO ₂ production in day 2	17–32% release of biomass	e
Silty clay loam	-	6.9%	1	10	-	Flush of CO ₂ production in day 2	27–58% release of biomass	e
Loam	12.5	1.5%	4	80	-	↑ CO ₂ (25–33%) with successive WDCs	↓ in dry period and recovered with each WDC	f
Sandy loam ^p	8.2–12	0.7–2.6%	7	32	-	↑ CO ₂ , but only for the first WDC	-	g
Clay ^p	18	1.6%	7	32	-	↑ CO ₂ , but only for the first WDC	-	g
Sandy loam	-	2.6%	6	42	-	No effect	-	h
Sand	10–22	1.2–5.3%	8–16	260–510	-	↑ (12–30%) increase in the mineralization of organic C during the first 200 days	↓ after drying	i
Sand	19.6	3.1%	60	168	-	↑ CO ₂ (50%). Effect ↓ with successive WDCs	↓ biomass and species	j
Birch leaves	-	-	1	60	-	↑ respiration lasting 12 h after rewetting	-	k
Silt loam ^o	-	-	4	74	-	↑ in 1st and 2nd WDC, but ↓ after 3rd	↓ Biomass C with WDC	l
Silty clay	8.2–12.9	1.4–3.3%	1–3	8, 16, 24	↑ with successive WDCs	↑ with successive WDCs	-	m
Silty clay loam	10.8	3.1%	1–3	8, 16, 24	↑ with successive WDCs	↑ with successive WDCs	-	m
Clay	10.7	1.1%	1–3	8, 16, 24	↑ with successive WDCs	↑ with successive WDCs	-	m
Loam	13	3.9%	1, 2, 4, 6, 9, 15	60	↑ potential nitrification with the number of WDCs	↑ after WDCs 4, 6, 9 and 15, but less pronounced with the number of cycles	No effect	n

Table 1 (continued)

Substrate type	C/N ratio	%C	No. of WDCs	Incubation period (days)	Net N mineralization	C mineralization	Microbial biomass	Reference
Clay loam	10	2.0%	1, 2, 4, 6, 9, 15	60	potential nitrification with the number of WDCs	↓ in the 15th WDC. Not affected in others	No effect	ⁿ
								^a Birch 1958 ^b Cabrera 1993 ^c Birch 1964 ^d Davidson 1992 ^e Kieft et al. 1987 ^f Botner 1985 ^g Adu and Oades 1978 ^h Degens and Sparling 1995 ⁱ Sorensen 1974 ^j Jager and Bruins 1975 ^k Clein and Schimel 1994 ^l Denef et al. 2001 ^m Agarwal et al. 1979 ⁿ Fierer and Schimel 2002 ^o Soils were mixed with senescent plant material before incubation ^p Soils were mixed with glucose and starch before incubation

rewetting cycles may cause the disruption of soil aggregates, exposing physically protected organic matter (Adu and Oades 1978; Lundquist et al. 1999), and increasing the accessibility of substrate that can be rapidly mineralized (Fisher et al. 1987; Jackson et al. 1988; Davidson et al. 1993; Appel 1998).

The range of the responses in Table 1 may be explained, in part, by the different temperatures reached during the drying phase (between ambient and oven-dried temperatures at 110°C), the duration of the drying period, and the time between wetting and drying cycles, which can affect the production of water-soluble substrates and the survival of microbial populations (Fierer and Schimel 2002). The number of wetting-drying events alters the overall ecosystem response, with a number of studies showing a continued increase in C and N mineralization with successive wet-dry cycles, while others showed diminished response after a single wet-dry cycle. More importantly, however, is that the size of the flush of carbon and nitrogen produced from these wet-dry cycles appears to depend in large part on the labile C and N soil pools (Tables 1, 2, Van Gestel et al. 1993; Schaeffer et al. 2003). In both field and laboratory studies, the increased substrate availability in finer textured soils, due to higher organic matter content, resulted in a qualitatively larger response to wet-dry cycles than in sandy soils with low organic matter content.

While many fewer studies have focused on the effect of wet-dry cycles on phosphorus cycling, Lebedjantzev (1924) observed almost 80 years ago that repeated drying and moistening of a soil brought about a substantial release of P, in addition to the more well documented release of inorganic N. More recently, Turner and Haygarth (2001) found an increase in the amount of water-soluble phosphorus in grassland soils as a consequence of drying and rapidly rewetting the soil. This phosphorus was predominantly in organic form and was positively correlated with the microbial-P biomass. The authors suggested that this newly available P was derived from soil microbial biomass, and was released by osmotic shock and cell lysis upon rewetting of the soil (Turner and Haygarth 2001). Another study supports the connection between microbial P and P release, where the size of the flush of inorganic P after rewetting a dry soil was strongly correlated with microbial P before rewetting (Grierson et al. 1998). In contrast, Cui and Caldwell (1997) analyzed the effect of wetting a dry soil in field conditions of a semiarid grassland, and they found that water pulses did not significantly affect phosphate concentration nor the mycorrhizal infection rate.

Microbial dynamics and control on the mineralization-immobilization balance of N

In water-limited ecosystems, N mineralization and immobilization by soil microbial communities are regulated primarily by three variables: (i) the ratio of C:N in organic substrates utilized by soil microorganisms; (ii) the N-use

Table 2 Consequences of wet-dry cycles (WDCs) on net N and C mineralization measured under field conditions

Site	C/N ratio	% C	No. of WDCs	Incubation period (days)	Net N mineralization	C mineralization	Microbial biomass	Ref.
Calcareous loam in Great Basin, USA	-	3.5%	1	45	↑ 50% in the second day, but declined in day 7	-	-	^a
Fine-textured soil in Great Plains, USA	10.5	2.0%	1	28	↑ with WDC, lower rates than the coarse-textured (see below)	-	-	^b
Coarse-textured soil in Great Plains, USA	8.57	0.6%	1	28	↑ with WDC, higher rates than the fine-textured (see above)	-	-	^b
Loamy sand soil in Jornada Desert, USA	-	-	1 and 4	192	↓ N mineralization, ↓ with 4 WDCs than with 1 WDC	-	-	^c
Fallow virgin land	9.1	6.0%	1	60	-	↑ in first days after rewetting, then ↓ rapidly	-	^d
Bare soil, Negev desert, Israel	-	-	1	4	-	↓ first day after wetting. Equal to control at day 4	↑ in first day after wetting. Equal to control at day 4	^e
Sagebrush steppe Utah, USA	11.9	2.6%	1	1	↑ Net N mineralization and net nitrification, ↑ Gross N mineralization and gross nitrification with WDC, ↑ NO flux within 5 min of WDC, For litter layer: ↓ Net N mineralization in spring and net N mineralization in summer	↑ CO ₂ flux within 5 min of rewetting	-	^f
Western Juniper woodland, Oregon USA	9.0	0.6%	1	1	↑ Net N mineralization and net nitrification, ↑ Gross N mineralization and gross nitrification with WDC, ↑ NO flux within 5 min of WDC	↑ CO ₂ flux within 5 min of rewetting	-	^g
Pinyon-Juniper woodland, New Mexico, USA	17.1	1.9%	1	1	↑ Net N mineralization in spring and ↓ Net N mineralization in late summer, ↑ Gross N mineralization and gross nitrification with WDC, ↑ NO flux within 5 min of WDC, For litter layer: ↓ Net N mineralization in spring and summer	↓ Net ↓ CO ₂ flux at 5 and 60 min of rewetting	-	^g

^aCui and Caldwell 1997^bSchimel and Parton 1986^cFisher et al. 1987^dBirch 1958^eSarig and Steinberger 1993^fSmart et al. 1999^gStark et al. 2002, Stark and Hart, unpublished data

efficiency of the microbial community; and (iii) the growth efficiency, or C-use efficiency, of the microbial community. Microbial grazing by protozoans, nematodes, and other metazoa also causes N mineralization by promoting turnover and release of bacterial and fungal N (Clarholm 1985); however, in this section we will focus on the effect of water pulses on activity of soil bacteria and fungi.

The C:N of microbial substrates, microbial N-use efficiency, and microbial growth efficiency (GE) interact to regulate N mineralization and N immobilization rates over a broad range of conditions. Of these three factors, the C:N ratio of microbial substrates probably has the largest impact on the balance between N-mineralization and immobilization because C:N ratios vary widely among different substrates (Fig. 2). For example, dead microbial biomass may have a C:N as low as 4:1, whereas the C:N of roots ranges from 30:1 to 70:1, and the C:N of woody branches from desert shrubs may be greater than 100:1. Microbial substrates with low C:N will contain more than enough organic N to meet microbial N demands, and the excess N will be mineralized; whereas high C:N substrates will lead to immobilization of N (Fig. 2). Seasonal changes in substrate C:N may occur following litterfall, root senescence, turnover of microbial biomass, or release of protected soil organic matter. For example, soil moisture pulses cause release of microbial cytoplasm into the soil solution (Kieft et al. 1987) and release of non-microbial soil organic matter (Appel 1998). Microbial degradation of these low C:N materials results in N mineralization, and may explain the commonly observed pulse of mineralization following wetting of arid and semiarid soils (Tables 1, 2, Birch 1958, 1959; Bloem et al. 1992; Zaady et al. 1996b; Cui and Caldwell 1997); however, if soil wetting follows addition of high C:N organic matter, N immobilization would be stimulated (Recous et al. 1990; Appel 1998). This explains the tendency for litter layers to immobilize N following wetting, even while the mineral soil is mineralizing N (Table 2).

Microbial N-use efficiency (the amount of N necessary to produce one unit of microbial biomass C) is essentially the inverse of the C:N of microbial tissue, and is determined to a large extent by the structure of the soil microbial community. Bacteria produce biomass with a lower C:N ratio than fungi (Paul and Clark 1996), and thus immobilize more N per unit of C assimilated than fungal-dominated communities. The microbial community structure may shift with season. Fungi are generally more tolerant of desiccation than bacteria (Adebayo and Harris 1971; Wilson and Griffin 1975), and thus the relative abundance of fungi may increase during the dry season. Such a shift in community structure, and thus N-use efficiency, may partially explain the tendency for slow rates of net N mineralization during dry seasons of many ecosystems. The response of mineralization or immobilization to a wetting event, however, may be determined by the relative growth rates of bacterial and fungal populations following wetting. For example, if bacterial popula-

tions expand first, followed by expansion of fungal populations, one would expect an initial phase of immobilization to be followed by a milder phase of immobilization or even mineralization.

Microbial growth efficiency (GE) is also likely to influence the mineralization-immobilization balance because it shows large temporal variation. The GE is the fraction of the organic C utilized by microorganisms that is actually converted into microbial biomass (as opposed to being respired as CO_2). The greater the GE, the greater the N-demand, and the more likely the N content of organic substrates will not meet microbial needs. Thus, high GE will promote N immobilization of inorganic N, whereas low GE will promote N mineralization. Microbial GE tends to be greatest (0.3–0.8) when environmental conditions are optimal for growth, and lowest (<0.1) when microbial populations are growing slowly, or not at all, and must use substrate supplies to meet maintenance energy requirements. Seasonal shifts in GE partially explain the slow accumulation of inorganic N in dry soils (low GE under adverse conditions) and the draw-down of inorganic N pools in continuously moist soils (high GE under optimal conditions). If a sudden water pulse in a dry soil results in an increase in available nutrients to the microbial community, high GE should promote N immobilization. However, if nutrient supplies become rapidly depleted GE would soon decline, and a phase of N mineralization would begin. Changes in GE appear to be less important in regulating the mineralization-immobilization balance in fungal-dominated communities than in bacterial-dominated communities.

The observation that wetting of dry soils usually stimulates a phase of net N mineralization (Tables 1, 2) suggests that the C:N of microbial substrates is the dominant factor regulating the mineralization-immobilization balance; and that drying-wetting cycles stimulate release of organic matter with a low C:N. However, to

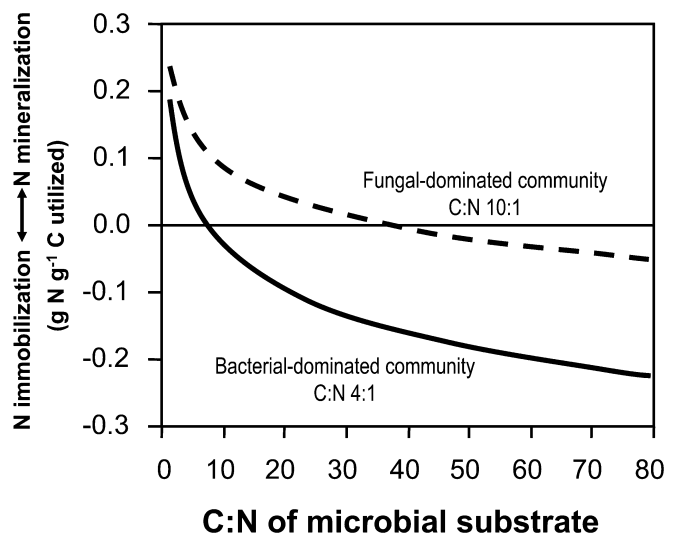


Fig. 2 The role of microbial community structure, and substrate characteristics in regulating N-mineralization and immobilization rates in soil microsites. Depicted are the relationships occurring at maximum microbial growth efficiency (GE)

obtain a more complete picture of factors regulating N mineralization, soil heterogeneity must also be considered. Soil microsites may differ widely in substrate C:N (Van Groenigen et al. 2002), as well as microbial GE and N-use efficiency. Differential inputs of litter from aboveground vegetation and roots concentrate the labile pools of C and N in vegetated patches (Vinton and Burke 1995; Kelly et al. 1996; Hook and Burke 2000). Fine-scale microsite variability may allow N mineralization and immobilization to occur simultaneously in even small soil volumes (Chen and Stark 2000). These patches may be large enough to be exploited by plant roots or mycorrhizae, or the net mineralization rate in several patches may determine N-availability to plants following water pulses.

Inverting the inverse texture hypothesis

The inverse texture effect introduced by Noy-Meir (1973) suggests that soil texture in arid and semiarid ecosystems plays a pivotal role in determining the efficiency of water uptake by plants, due to the effect of texture on soil evaporation. In arid zones, evaporation from the upper layers—rather than free drainage from subsurface horizons—causes the largest loss of soil moisture. Sandy soils have less runoff and more infiltration. Because of lower water holding capacity, infiltration is deeper and loss by evaporation is smaller. As a result, primary production in very arid regions should be greater on coarse-textured than on fine-textured soils due to relatively higher water availability in sandy soils. Sala et al. (1988) tested the inverse texture hypothesis synthesizing a large data set and developed an empirical regression model for the Great Plains region of North America. The authors found that when annual precipitation was less 370 mm, sandy soils were more productive than loamy soils of finer texture. At the same time, when annual precipitation exceeded 370 mm, the model predicted that sandy soils would be less productive than fine-textured soils (Fig. 3A).

But how does the inverse texture effect apply to belowground processes? Several studies have examined the effect of soil texture on ecosystem processes in arid and semiarid ecosystems (Herlihy 1979; Schimel and Parton 1986; Burke 1989; Burke et al. 1989; Van Veen and Kuikman 1990; Hook et al. 1991; Hassnik 1997; Strong et al. 1999; Hook and Burke 2000; Kaye et al. 2002) and modeled results show a marked soil texture effect on soil moisture dynamics in semiarid shrublands (Fernández-Illescas et al. 2001). Studies in the Great Plains of North America have shown that total C and N pools positively correlated with clay content (Kaye et al. 2002), and that most parameters of biogeochemical cycling, including total C and N, particulate organic matter, and mineralizable C and N in soils from shortgrass steppe were negatively correlated with soil sand content (Hook and Burke 2000). In addition, fine-textured soils tend to increase water-holding capacity (Hook and Burke 2000), which means that water availability is greater at the soil surface, where the vast majority of microbial activity

occurs (Foster 1988). Fine-textured soils have the capacity to preserve or protect organic matter and microbial biomass, which may allow greater nutrient retention (Van Veen et al. 1984; Gregorich et al. 1990). As a result, N mineralization is often greater in fine-textured soils than coarse-textured soils under the same climatic conditions, demonstrated both for empirical studies (Appel 1998; Degens 1998) and modeling results (Fernández-Illescas et al. 2001).

These studies suggest a corollary hypothesis for the effect of soil texture on belowground processes in water-limited ecosystems, which is different than for primary production (Fig. 3B). Fine-textured soils reduce water availability for primary production due to increased evaporative losses in arid ecosystems (<370 mm; Sala et al. 1988; Fig. 3A), but finer-textured soils in the same climatic regime may actually experience increased nutrient availability relative to coarse-textured soils. We suggest that N mineralization would increase linearly along a gradient of precipitation in coarse-textured soils concurrent with increasing soil C and N pools and increasing water availability, whereas fine-textured soils would show a saturating relationship due to the interaction of pool size and water availability.

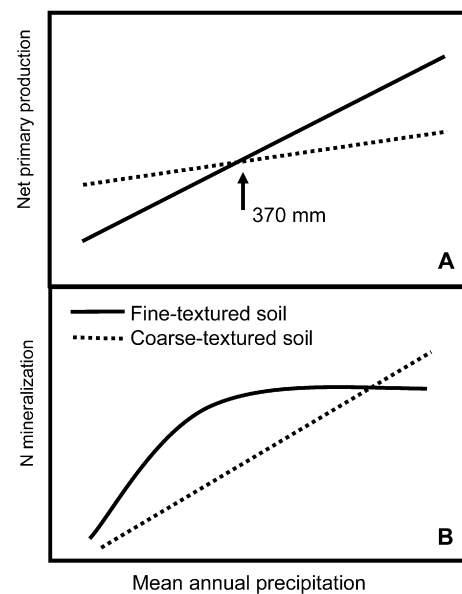


Fig. 3 Relationship between soil texture and ecosystem processes along a gradient of precipitation. **A** Relationship between mean annual precipitation and net primary production as hypothesized by Noy-Meir (1973) and empirically demonstrated by Sala et al. (1988). The point at which the lines cross for fine- and coarse-textured soils comes from regressions developed in Sala et al. (1988). **B** Hypothesized relationship of the effect of soil texture on N mineralization along a gradient of precipitation, which differs from the relationship with net primary production. In coarse-textured soils, N mineralization increases linearly along a precipitation gradient due to increased water availability and increased C and N pools. In fine-textured soils, N mineralization increases much more rapidly due to increased water holding capacity, and turnover and size of C and N pools. The difference between soil textures diminishes in humid sites, and the effects on water retention and C and N pools are dampened

The difference in *potential* N mineralization between coarse- and fine-textured soils would be greatest in arid ecosystems due to the relative difference in soil water holding capacity. However, more important than the direct effect of water availability on microbial activity would be the change in the overall size of the C and N pools due to increased NPP inputs (Amundson et al. 1989; Austin and Sala 2002). Thus, along a gradient of water availability, the *realized* changes in N mineralization under very arid conditions would be small due to small soil C and N pools, in spite of the importance of soil textural differences (Fig. 3B). The effects of soil texture would be most pronounced, however, in semiarid to subhumid conditions, where soil pools of C and N are larger and the differences between N turnover are greater between coarse- and fine-textured soils (Groffman and Tiedje 1988). Finally, in subhumid conditions where flooding frequency may result in periodic anoxic soil conditions, the coarse-textured soils would show increased N mineralization when compared to fine-textured soils. By inverting the inverse texture hypothesis, it appears that soil texture, water pulses, and labile C and N pools interact in different ways to affect belowground processes than aboveground primary production.

Water pulse effects on nitrogen inputs and loss

A unique aspect of many arid and semiarid ecosystems is the presence of biological soil crusts, a complex soil surface community dominated by cyanobacteria, micro-fungi, mosses, and lichens. They cover the top 1–2 mm of the soil surface between the vascular plant cover, and become metabolically active immediately upon wetting. The presence of cyanobacteria and lichens in these soil crust communities results in the fixation of nitrogen, and may represent the principal input of new N in some desert ecosystems due to low rates of atmospheric deposition and heterotrophic fixation (Evans and Ehleringer 1993; Evans and Belnap 1999). Most desert precipitation events are pulses of less than 3 mm (Loik et al. 2004), an amount too small to elicit a response from most vascular plants, but large enough for a response from these crust communities. For larger rainfall events, crusts may reduce the rate of soil drying, giving vascular plants more time to respond to increased water availability (George et al. 2003). Each species within the crust community has a different physiological response to wetting, and their relative abundance and the nature of the water pulses determine the influence of crust communities on carbon and nitrogen dynamics in desert soils (Jeffries et al. 1993; Castenholz and García-Pichel 2000; Lange 2001). Much of the carbon fixed by these communities is highly labile and is leaked into the surrounding soil. At the same time, N inputs through fixation are occurring; annual estimates range widely (reviewed in Belnap 2001), but in general are linked to the amount of time the soil crusts are wet and able to maintain activity. For example, recent estimates from the Colorado Plateau show inputs ranging from 1–

10 kg/ha/year, with inputs from lichens greater than cyanobacterial species (Belnap 2002). The effects of water pulses on crust carbon and nitrogen fixation are mediated by temperature, primarily because cool desert soils are wet longer than hot desert soils and temperatures are more often optimal, resulting in higher N inputs in cool deserts. A large fraction (up to 70%) of the nitrogen fixed by the crust communities is also released into the surrounding soils, particularly after a long dry period, which then becomes available to plants and microbial soil communities (reviewed in Belnap 2001). This demonstrates the tight linkage between N and C inputs from soil crust communities and the nature and magnitude of water pulses.

Losses of N in water-limited ecosystems are not well understood, but consist of gaseous losses through N transformations as well as runoff and deep percolation. Wetting of dry soil has strong effects on emissions of NO (Davidson 1992), with the highest NO flux rates in field studies occurring during the 24 h immediately following wetting during the summer, when temperatures are relatively high (Davidson et al. 1993; Smart et al. 1999). Wetting of dry, warm soils in a sagebrush steppe of Utah increased NO emissions by as much as 400-fold (Smart et al. 1999). In fact, the NO emissions following moisture pulses may represent a substantial proportion of the total annual NO flux (Yienger and Levy 1995). NO fluxes have also been shown to increase along a gradient of increasing aridity (Stark et al. 2002). While ambient NO flux rates are slow and difficult to predict, the rapid fluxes following soil wetting showed a strong negative correlation with C-availability and microbial demand for N. Additionally, NH_4^+ concentrations may limit flux of NO from desert soils during wetting events (Hartley and Schlesinger 2000). Soils low in organic C appeared to have lower rates of NO consumption, leading to greater rates of NO emission from soils of more arid ecosystems (Stark et al. 2002).

Nitrification and denitrification are considered to be the most important sources of N_2O from soils (Paul and Clark 1996). Mummey et al. (1994) examined the sources and regulation of N_2O in a shrub steppe in North America and found that along a gradient of soil moisture, N_2O fluxes were maximum with intermediate soil moisture (50% of water holding capacity) and that the source was primarily due to nitrification. In addition, as a result of experimental wet-dry cycles, Mummey et al. (1994) found that relatively large pulses of N_2O and N mineralization occurred in the soil during the subsequent 60 h after wetting. N_2O flux in this shrub-steppe ecosystem is regulated by interactions between soil water content and the balance between N mineralization and N-immobilization.

Because denitrification can proceed at high rates during brief windows of high water and nutrient availability, pulse dynamics play an important role in this process in arid and semiarid ecosystems. While it was believed that desert ecosystems are unsuitable for the conditions necessary for denitrification, given infrequent periods of

adequate water availability, denitrification can occur at rates comparable to temperate ecosystems (Virginia et al. 1982; Peterjohn and Schlesinger 1991; Groffman et al. 1993; Zaady et al. 1996a). The denitrifying enzyme content in soil represents a persistent pool capable of tolerating extended periods of desiccation; such tolerance allows denitrifiers to respond rapidly to favorable conditions (Peterjohn and Schlesinger 1991). Thus, pulses of water availability may create conditions for denitrifying activity where adequate carbon substrate and soil nitrate accumulate during inter-pulse periods. Wetting-drying cycles appear to accentuate denitrification, which strongly correlate with pulses of C and N mineralization in the wet-up period of wet-dry cycles (Groffman and Tiedje 1988). This appears to be a previously underestimated parameter for N loss (Frank and Groffman 1998), and water pulses appear to be critical for the occurrence of denitrification in water-limited ecosystems.

Water versus nitrogen limitation in arid and semiarid ecosystems—is there a pulse connection?

There is evidence to suggest that at the regional scale, nitrogen availability in addition to water availability may contribute to limitation of net primary production in arid and semiarid ecosystems (Fisher et al. 1988; Gutiérrez et al. 1992; Burke et al. 1997; Belnap 2001; Austin and Sala 2002). In grassland ecosystems, modeling dynamics of C and N pools have demonstrated a correlation between water and nitrogen limitation (Parton et al. 1987, 1988; Schimel et al. 1996, 1997). Moreover, these results demonstrate that although biophysical processes have “memory” effects of at most 1 or 2 years through soil moisture storage, the coupled dynamics of water, carbon, and nitrogen in the soils can induce lag effects over decades through the decomposition of soil organic matter. In the short-term, the activity of soil microbes may be less sensitive to low soil water potential than is water uptake by plants (Singh et al. 1989; Austin 2002), and many small rain events may be of insufficient magnitude to elicit a plant response but can cause a rapid increase in activity of soil organisms (Freckman et al. 1987; Schwinning and Sala 2004). Thus, soil microbes may continue to be active in moments when plants are not, reducing competition for mineral nitrogen and increasing the immobilization in microbial biomass (Singh et al. 1989; Bolton et al. 1993).

One consequence of the frequently observed flush of N mineralization in surface soil layers after wetting events is the accumulation of inorganic N during subsequent dry periods (Fig. 1). This relationship may result in periods of maximum water and soil nutrient concentrations occurring at different moments during the year, with periods of high inorganic nutrient concentrations, while plants are either senescent or unable to respond to nutrient pulses (Jackson et al. 1988). This asynchrony may be enhanced in areas where the growing season does not occur during the season of maximum rainfall (e.g., cold deserts, Mediterranean zones), or where periods of maximal N input do not

coincide with growing season, such that the temporal difference between nutrient mineralization (supply) and plant demand is amplified. These temporal differences increase the possibility of nutrient loss through runoff or deep percolation.

The increased potential for loss under these conditions of incongruous nutrient supply and demand in the short-term could lead to a N cycle in the long-term in which losses relative to pool sizes are greater, driving toward systematically low N availability (Austin and Vitousek 1998; Vitousek et al. 1998; Austin and Sala 1999). The accumulation of mineral N in the soil increases potential for leaching losses, which has been shown to accumulate in the deep soil layers below the rooting zone in desert ecosystems (Walvoord et al. 2003), or loss through ammonia volatilization and denitrification. Additionally, brief periods of unusually wet weather could reduce N availability by promoting denitrification. While these losses may be relatively small in terms of annual turnover, the cumulative effect may have large impacts on C and N pools (Peterjohn and Schlesinger 1990; Schlesinger et al. 1990). In spite of low N demand by vegetation, the asynchrony results in high loss potential, particularly for inorganic N, resulting in low N retention potential and a higher proportional loss of mineral N relative to more humid ecosystems (Austin and Vitousek 1998; Vitousek et al. 1998; Handley et al. 1999; Amundson et al. 2003). Thus, water pulses may play a critical role for the maintenance of low N supply in arid and semiarid ecosystems.

Human impact and global change in pulsed environments

Increased drought periods, shifts in the wet-dry cycles of soils, or increases in extreme events will alter biogeochemical cycles, particularly nitrogen cycling, in natural ecosystems (Ryan et al. 1998). Altered frequency or size of pulsed water events may also affect the potential for invasions, as species which are better adapted to an altered climate may have an advantage over native vegetation (Mack et al. 2001). In particular, changes in vegetation structure, particularly changes in the shrub-grass ratio, could result in increased spatial heterogeneity of resources (Schlesinger et al. 1996; Kieft et al. 1998) or, alternatively, increase vegetative cover and fire frequency (D’Antonio and Vitousek 1992; Evans et al. 2001), which may respond to pulsed water events in novel ways from undisturbed ecosystems.

Increased gaseous emissions of NO, N₂O and NH₃ from deserts due to changes in precipitation regime or increased desertification may contribute to the depletion of stratospheric ozone, the global greenhouse effect and the regulation of rainfall acidity. Nitrous oxide, in particular, is cause for concern, as it is a stable compound in the troposphere with a long residence time and absorption properties that make it an extremely effective greenhouse gas with a radiative forcing factor of nearly 300 times that

of CO₂ (IPCC 2000). The concentration of N₂O in the atmosphere has risen significantly since the beginning of the century and is currently increasing by 0.3% year⁻¹ (Matson and Vitousek 1990; IPCC 2000). Arid lands cover approximately 40% of the Earth's surface, and while the estimates for gaseous N emissions from desert ecosystems are relatively low when compared to tropical ecosystems (Davidson and Kinglerlee 1997; Hartley and Schlesinger 2000), the large expanse of aridlands results in the potential for global impacts due to increased N gaseous losses from these ecosystems (Schlesinger et al. 1990).

The interaction of multiple global change drivers, including changes in precipitation regime, elevated CO₂, changes in temperature, and patterns of N deposition will interact in ways that may be difficult to predict based on the response of a single driver alone (Shaw et al. 2002), but the nature of pulsed water events needs to be incorporated into our understanding of ecosystem functioning in arid and semiarid ecosystems in order to better forecast human impact in the next century. It appears that pulsed water events play a key role in a number of belowground processes in arid and semiarid ecosystems, and that changes in the nature of pulsed events due to human impact may be more important than larger-scale changes in total rainfall or temperature in affecting biogeochemical cycling in water-limited ecosystems.

Approaches to understanding pulse dynamics and biogeochemistry

Rainfall in arid and semiarid ecosystems is highly variable in space and time, and while the characterization of pulses have been described, the consequences on element cycling and plant responses are more complicated to determine. A multitude of approaches is necessary to disentangle the various effects that pulses of water have on biogeochemical cycling, and to identify mechanistic explanations for the controls of pulsed water availability on ecosystem processes.

One of the approaches is the manipulation of the pulse itself, modifying the amount and timing of water inputs and monitoring its effects on the status and processes of the principal ecosystem processes. Possible manipulations include rainfall exclusion, rainfall supplementation by irrigation systems and/or a combination of both, and can be made in mesocosm, greenhouse or field conditions. In field experiments, water exclusion usually involves the use of mobile (functional only during rainy periods) (Stansell and Sparrow 1963) or fixed (Yahdjian and Sala 2002) rainout shelters to reduce or eliminate natural precipitation events. In addition, artificial rainfall systems can be designed in a variety of ways to meet experimental goals, including the manipulation of size of water pulses, frequency between events, and total rainfall. Combined fixed-location rainout shelters with irrigation systems to redistribute water fallen on shelters permits the creation of multiple precipitation treatments, with almost no changes

in water quality in the water supplemented plots (Fay et al. 2000; Knapp et al. 2002).

Stable isotope studies using pool dilution and chaser studies show great promise in elucidating the relationships between water pulses and biogeochemical cycles (Stark 2000). Studies using labeled nitrogen and water sources (with ¹⁵N or ²H) can be applied in conjunction with water manipulations to examine parallel effects on carbon and nutrient cycling (Gebauer and Ehleringer 2000). Using labeled plant material with ¹⁴C or ¹⁵N for tracing the movement of carbon and nitrogen during wet-dry cycles (e.g. Bottner 1985; Van Veen et al. 1985; Smith et al. 1989; Bottner et al. 1998) has been very useful in advancing our understanding of the nature of carbon-nutrient interactions. Recently, changes in natural abundance of ¹³C and ¹⁵N are being used to better understand the response of water-limited ecosystems to global change, such as elevated CO₂ (Billings et al. 2002; Van Groenigen et al. 2002).

Finally, heuristic and mathematical models to track the 'untrackable' variables that occur at very rapid time scales, or are very difficult to measure in the field (i.e. leaching losses) or laboratory, allow for predictions and identification of key parameters for future research. These models can describe, at the daily and sometimes even at the hourly time scale, the coupling of soil carbon and nitrogen dynamics with soil moisture and temperature that act as their main forcing variables. Recently, Porporato et al. (2003) and D'Odorico et al. (2003) developed a stochastic model to investigate the hydrological mechanisms controlling the soil nitrogen cycle at the daily time scale. These results showed how fluctuations of random precipitation affect carbon and nitrogen dynamics at different time scales, from the low-frequency dynamics of changes in soil organic matter, to the high-frequency variability of leaching and plant uptake. Mathematical models and numerical simulations provide a valuable tool of investigation which is complementary to field and laboratory experiments for disentangling these multiple effects of pulsed water on ecosystem processes.

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