## Chapter 15 Biological Phosphorus Cycling in Dryland Regions

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## 15.1 Introduction

Drylands consist of arid, semiarid, and subhumid grasslands and shrublands (Fig. 15.1). These landscapes comprise over 40% of terrestrial lands, with over 1 billion people depending on them for their livelihoods. Thus, understanding and maintaining the fertility of these ecosystems is essential to human well-being. Water and nitrogen (N) have long been thought to be the major factors limiting primary productivity in dryland ecosystems (Hooper and Johnson 1999). However, studies are now showing that phosphorus (P) can be at least equally, or even more, limiting than N in many dryland ecosystems, especially in high-pH and calcareous soils (e.g., Ma et al. 2007; James et al. 2005; Lajtha and Schlesinger 1986). The biological cycling of P in drylands has many differences from cycling in more mesic ecosystems. In this chapter, I will discuss the major sources of P in drylands, how this P is redistributed, the abiotic and biotic controls on P availability (measured as resin or bicarbonate-extractable P), how available P affects native plant distribution and exotic plant invasion, and how climate change is expected to influence P availability in dryland soils.

## 15.2 Inputs and Losses of P in Drylands

In dryland regions, P inputs into soils are primarily the result of the deposition of atmospheric dust, and secondarily are a result of the new weathering of parent materials (Fig. 15.2). Dust deposition into these regions is highly variable in space and time. Dust inputs to the Colorado Plateau and Mojave Deserts, USA, for the past 25 years show annual inputs of 20–40 g m<sup>2</sup> per year. Inputs in other dryland

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Fig. 15.1 Drylands of the world. The *light-colored* regions indicate drylands, which include the hyperarid, arid, semiarid and subhumid grasslands and shrublands of the world



**Fig. 15.2** Important processes that control the distribution and availability of P in dryland regions. These include the input and losses of P, vertical and horizontal redistribution of P-containing materials, and the factors that control P bioavailability (BSC = biological soil crust)

regions range from <1 to 276 g m<sup>2</sup> per year, with most values falling between 6 and 20 g m<sup>2</sup> per year (for a review, see Reheis and Kihl 1995). As most of this dust consists of fine-textured materials, it can contain a significant amount of P, ranging from 0.01% to 5% in the western USA (Reynolds et al. 2006a, b, c; Reheis et al. 1999).

Dust also collects on plant leaves, and when washed off it can significantly increase P in soils under plant canopies, with one study showing 24% of soil P coming from canopy dust capture (Callaway 2007). On a global scale, dust deposition is far higher in the semiarid steppes of Africa and Eurasia than North America (Okin et al. 2004; Field et al. 2009).

Deposited dust is retained at sites where soil surfaces are protected by high plant cover or where soils are covered by rocks, physical crusts (formed by silt, clay, and/ or salts), or biological soil crusts. High cover of small gravel (2.5 cm) maximizes dust capture (Li and Liu 2003). Physical crusts that are generally hard and flat tend to not capture and retain dust unless wet. Biocrusts are also important in capturing dust. Biocrusts are communities of cyanobacteria, mosses, and lichens that cover the top 1 cm of most dryland soil surfaces. In SE Utah, USA, biocrusted soil surfaces had 2.6 times greater total P than soils 2–5 cm below them (271 vs. 104 ppm P, respectively) (Reynolds et al. 2001). Biocrusts have been shown to effectively capture dust in a variety of desert environments (Verrecchia et al. 1995; also reviewed in Belnap 2003a) because the organisms are sticky. Depending on the environment, they can create soil pinnacles up to 15 cm high (Fig. 15.3) and often have moss and lichen tissue projecting upwards from the soil surface (Fig. 15.3). In California, USA, lichens and mosses were observed to trap 0.15 kg sediment ha<sup>-1</sup> per year (Nash 1996).

Rock weathering occurs at the surface because differential insolation cracks. In cooler deserts, rocks at the surface experience freeze–thaw action as well. Wind abrasion is also high in this environment. The erosion rate of rock by water is low in drylands because overland water flows are infrequent and highly localized. Fungi, cyanobacteria, and lichens contribute to weathering of surface rock, and fungi to weathering at depth. These organisms tunnel along crystal planes, cleavages, cracks, and grain boundaries in rocks, especially in sandstone, dolomite, calcite, and some granites. They crack rock with osmotically generated turgor pressure (Gadd et al. 2007). They also form carbonic acid during respiratory activity and excrete metal-complexing metabolites and organic acids (e.g., oxalate, citrate,



Fig. 15.3 *Left*: well-developed biological soil crusts. Note the many crevices that trap P-containing materials, including organic matter and dust. *Right*: a thin section of moss, showing dust trapped within the moss shoots. (Photo courtesy of D. Eldridge)

malate, succinate, gluconate), all of which dissolve rock material while also increasing bioavailable P (Jones and Oburger 2011).

### 15.3 Distribution and Redistribution of P in Drylands

Because most P inputs occur at the soil surface via dust, weathering, and the deposition of plant litter, P is concentrated in surface soils in most environments (Jobbágy and Jackson 2001). This is especially pronounced in drylands because there is insufficient rainfall for subsequent downward leaching of P into soils (Charley and Cowling 1968; Jobbágy and Jackson 2001; Charley 1977). For instance, P concentration was 900–1,100 ppm at 3 cm, decreasing to 500 ppm by 29 cm depth in northern Utah, USA (Jurinak and Griffin 1972). However, one study in the arid regions of southwestern USA found equally high levels of P at 2–3 m depth as found at the surface at one of their three sites (McCulley et al. 2004).

Despite the input of P via dust occurring fairly evenly over a given area, redistribution of soil P by wind, water, and animals is common in dryland regions. The large spaces between plants allow for soil movement by wind and water. The consumption of forage in one place & movement to free water can result in moving P over large distances. This redistribution of P can determine the composition, biomass, and distribution of a given plant community, which in turn influences animal distributions. In an amplifying feedback cycle, dryland plants heavily influence the spatial distribution and the availability of P through capture of surface materials and the exudation of compounds that solubilize otherwise biounavailable P.

## 15.3.1 Horizontal Redistribution of P and Materials Affecting P Availability

#### 15.3.1.1 Wind

Dryland regions are dominated by a low cover of short plants, and are generally characterized by constant and often high winds. Left undisturbed, most desert soils are well-stabilized by the presence of rocks, physical crusts, and/or biocrusts, which confer substantial resistance to movement of surficial materials (Belnap et al. 2006). However, when plant cover is low (whether naturally or postdisturbance) and these protective covers are disturbed by grazing, plowing, off-road vehicles, or other activities that disturb the soil surface, the soils are easily mobilized and high amounts of P can be lost or redistributed (Fig. 15.4) (Neff et al. 2005; Hiernaux et al. 1999).

Disturbed dryland soil surfaces can produce up to 15 times or more sediment compared to undisturbed soils (Field et al. 2009). Larger particles are moved to the



**Fig. 15.4** (a) Total sediment loading increased in high elevation lakes after about 1850, coinciding with the intensification of agricultural activities (e.g., plowing, livestock grazing) in drylands of the western USA. The Taylor Grazing Act, enacted in 1920, controlled livestock numbers and resulted in a decline in dust deposition. These data are from two lake cores, Porphyry Tarn and Senator Beck Tarn. (b) Levels of P showed a similar sudden surge in sediment loading with the arrival of intense agriculture, showing how land disturbance has accelerated the vertical transport of P. However, unlike sediment, P loading has continued to increase over time (after Neff et al. 2008)

nearest obstruction (e.g., rocks, plants, biocrust mounds, base of hills, or depressions, or are lost from the system if plant materials accumulate under plants). This can lead to the often observed "islands of fertility" under shrubs (Schlesinger et al. 1990). However, in a review of 49 studies comparing soil chemistry of 127 plant/ interspace pairs, soil P (some studies measured total P, some measured available P) was more often elevated in the interspace soil than under the plant canopy, whereas carbon and N were elevated under the plant canopy in 82 and 68% of the comparisons, respectively (Belnap unpublished results). In the studies where the increase in resources did occur under plants, many sites had highly disturbed interspaces. Under these circumstances, the increase in available P under the plant was probably correlated not only with the collection of P-containing plant and soil materials under the plant, but also with the increase in organic material because organic matter can increase P availability through four main mechanisms (1) increased soil C increases the abundance and activity of soil biota, which then decompose plant litter more rapidly; (2) greater organic matter increases water infiltration and soil moisture retention, thus allowing for longer times of microbial and plant activity (Santos et al. 1978; Callaway 2007); (3) competition of organic anions for adsorption sites on calcite increases available P (Holford et al. 1990); and (4) organic matter can complex with Al and Fe, thus increasing bioavailable P (von Wandruszka 2006; Ma et al. 2009).

As organic matter content is often <0.3% in bulk dryland soils, its importance in keeping P bioavailable may be low (Lajtha and Schlesinger 1988), except in the localized patches under shrubs (Ma et al. 2009). When P does accumulate under plants, it can persist long after the plant is removed. Soils under shrubs in the southwestern USA that had been dead for 13 years still showed elevated P

(Klemmedson and Tiedemann 1986), and P accumulations under *Acacia papyrocarpa* were unchanged 50 years after shrub death in Australia (Facelli and Brock 2000).

Dust is also transported long distances by wind, including to nearby mountains or even across oceans, resulting in P loss at the local to the global scales (Fig. 15.2). A comparison of landscapes grazed for 150 years relative to never grazed lands shows a large depletion of P in grazed soils (Neff et al. 2005). Lake cores at high elevations of nearby mountains show that sediment inputs in the past 150 years (corresponding to the time when intense grazing and agricultural activities began in the western USA) relative to the past 3,000 years have increased five- to eightfold, with a concomitant four to five times increase in P levels (Fig. 15.4) (Neff et al. 2008), thus partially accounting for P lost from lower elevation soils.

#### 15.3.1.2 Water

Over long time periods, water redistributes smaller soil surficial materials from the tops of slopes to slope bases, resulting in higher concentrations of silt and clay, organic matter, and nutrients (including P) at lower landscape positions (Fig. 15.2) (e.g., Reynolds et al. 2006a; Bestlemeyer et al. 2006; Venter et al. 2003). This facilitates the growth of nutrient-demanding plants, especially annuals, and thus can determine plant community structure. Overland flow can also redistribute large amounts of surficial material in a short time period with intense rain events. Over days to millennia this material is lost from the local ecosystems. Much of this material eventually ends up in large rivers, which represent the main source of P for the oceans (Baturin 2003).

#### 15.3.1.3 Wildlife, Livestock, and Human Settlements

The activities of wildlife, livestock, and human settlements can also result in a substantial horizontal redistribution of P (Fig. 15.2). Wildlife and livestock often consume vegetation in one location whereas excretory processes may occur kilometers distant. Feces contain P, increase soil organic matter and water infiltration/retention, thus increasing total soil and bio available P. As P is highly conserved in soils and vegetation (Charley 1977; Woodmansee 1978), especially in places where animals congregate, including under trees, in feedlots, within wildlife territorial boundaries, along fence lines, and in preferred plant patches at water or mineral resources (Naiman et al. 2003; Bestlemeyer et al. 2006), P stays elevated in these patches for long time periods. Protective nighttime enclosures in Africa have up to 14 times the P concentration found in surrounding soils and, after abandonment, soil and foliar concentrations of P can remain elevated for 40 years or more (Augustine 2003; Charley 1977; Hilder and Mottershead 1963). In contrast, soils in the surrounding landscape experience a slow depletion in P over time, as it is translocated to the animal enclosures (Augustine 2003). After abandonment, these

areas of elevated P (and N) are preferentially used by livestock and wildlife, including birds, reptiles, and large and small mammals, whose fecal material helps maintain high P levels over time, reinforcing the landscape-scale heterogeneity of nutrient distributions (Bestlemeyer et al. 2006; Naiman et al. 2003; Palmer et al. 1999; Augustine 2003; Scholes 1990).

A wide variety of small mammals, large mammals, and reptiles also create many shallow surface pits or burrows that trap wind or waterborne litter, feces, seeds, and fine soil particles. These materials increase soil P. They also indirectly increase available P by increasing organic matter (Eldridge and Rath 2002; Whitford 2002).

Ants can move large numbers of seeds, leaves, and other materials from the surrounding landscape to their nests. For instance, it is estimated that the genus *Pheidole* moved ~ $1.6 \times 10^9$  seeds in one season at a site in New Mexico, USA (Whitford and Bestlemeyer 2006). In Wyoming, ants were estimated to have denuded 36,450 ha of dryland vegetation, while greatly increasing nutrients, including P, and productivity at nest edges (MacMahon et al. 2000). These ants generally leave the outer seed coat on the surface and take the rest of the seed underground. This seed material at the surface directly increases soil P, as well as enhancing available P through increased organic matter. Dung beetles, found in most dryland regions, can move large amounts of fecal material substantial distances from where the material was originally deposited (Naiman et al. 2003) (For more information on the role of macrofauna in soil P cycling see Chapuis-Lardy et al. 2011).

#### 15.3.2 Vertical Redistribution of P

The soil depth at which P occurs can determine its availability to biota because various organisms have differing abilities to reach various soil depths. For example, plant roots can explore soils much more deeply than soil surface mosses and lichens. Thus, vertical mixing of soils can have substantial ecosystem-level impacts. Although most vertical redistribution of P is due to animal activity, plants can also influence where P is located in the soil profile.

#### 15.3.2.1 Animal Activity

Digging activities of animals can carry soil, plant litter, seeds, feces, and cadavers down to >1 m depth or more. On the other hand, these same materials are often brought to the surface. Burrowing also creates large macropores that enhance water infiltration and, during overland flow events, allow surface plant litter and feces to enter the soil. However, dryland ecosystems vary widely in the number of animals that mix soils to depth. For instance, the Colorado Plateau region, USA, has very low numbers of rodents, termites, or ants and therefore very little vertical mixing compared to many other dryland ecosystems such as the Sonoran or Chihuahuan deserts (Belnap and Phillips 2001; Belnap et al. 2005; Whitford 2002). In addition, the occurrence of these animals can be spread widely or concentrated in specific areas. Therefore, the relative amount of P found at depth due to animal mixing varies widely at the local to regional scales.

#### 15.3.2.2 Ants and Termites

Ants and termites occur worldwide in drylands. They are among the most abundant animals in terrestrial habitats and are the dominant insects in many ecosystems (MacKay 1991). Various ant and termite species move different amounts and types of surficial materials and, as species vary among regions, the relative impact on vertical P distributions varies as well (see Chapuis-Lardy et al. 2011; Whitford and Bestlemeyer 2006). Globally, termites and ants move prodigious amounts of soils in dryland regions and are probably the most important group in the vertical redistribution of P in dryland soils. In Argentina, ants can move 1,100 kg soil ha<sup>-1</sup> per year from 150 cm depth to the surface (Lee 1977). In the Chihuahuan desert, ants carry soil from 200 cm deep to the surface and, combined with vertebrate burrowing, move sufficient subsurface soils to cover 20% of the soil surface (Whitford 2002). Large quantities of seeds and plant material are carried underground by ants, and their excretory products also accumulate at depth. Almost all studies show that long-lasting ant mounds have higher N, P, and organic matter than nearby nonmound soils, regardless of the continent or desert region, landscape position, soil texture, or other environmental factors (e.g., Wagner 1997; Lobry de Bruyn and Conacher 1990; Whitford 2002; Palmer et al. 1999). The creation of soil macropores results in higher infiltration rates than in surrounding soils (Whitford 1999, 2002). Ant nests have also been shown to support a higher number of soil organisms (e.g., bacteria, fungi, protozoa, mites, and collembola), which results in faster decomposition, thus resulting in higher soil available P (Wagner 1997; Boulton et al. 2003).

Termites can move up to 16,000 kg soil ha<sup>-1</sup> per year and affect up to 30% of the soil surface (MacKay 1991; Lobry de Bruyn and Conacher 1990; Wood and Sands 1978; McClaran and Van Devender 1995). They consume or move up to 90% of plant material and 100% of dung found on soil surfaces to depth, as well as depositing their own feces and carcasses at depth (McClaran and Van Devender 1995; Whitford 2002). As with ants, termite mounds have higher N, P, and organic matter than nearby nonmound soils, regardless of location or other environmental factors. Unlike ant mounds, some termite mounds will decrease water infiltration whereas others increase it (Whitford 2002). Many studies have shown that large herbivores preferentially utilize plants growing on the N- and P-rich soils of recently abandoned termite and ant mounds (e.g., Augustine 2003; Scholes 1990). As mentioned above, this results in further P enhancement due to dung and urine from these animals.

#### 15.3.2.3 Dung Beetles

Dung beetles remove voluminous amounts of dung from the soil surface and bury it to different depths, depending on the species (Naiman et al. 2003). In Kruger National Park, South Africa, there are over 120 species of dung beetles. Despite the vast quantity of dung deposited daily by wildlife, these insects remove the bulk of newly deposited dung, burying it underground as food for their larvae. This burrowing also creates soil macropores that facilitate water infiltration.

#### 15.3.2.4 Mammals and Reptiles

Mammals and reptiles (e.g., kangaroo rats, springhares, molerats, gerbils, aardvarks, badgers, foxes, porcupines, lizards, aardwolves, wombats, coyotes, woylies) create burrows for shelter and to find or cache food, thus vertically mixing soils and other materials to 1 m or more (Scholes et al. 2003; Palmer et al. 1999). Burrows can be so numerous in small areas that they are visible on LANDSAT images (Whitford 2002). Large amounts of subsurface soils are moved to the surface during burrowing. Australian woylies (also known as brush-tailed bettongs) can dig 5,000–16,000 new holes ha<sup>-1</sup> per year, moving over 13 tonnes of soil (Garkaklis et al. 2004; soil turnover estimations for other mammals are also listed in this publication). Heteromyid rodents in the Chihuahuan desert can create over 100,000 holes ha<sup>-1</sup> per year (Whitford 2002). Porcupines alone have been estimated to have impacted up to 4% of soil surfaces in the Negev Desert in Israel (Alkon 1999). Dust-bathing and mud-wallowing by large mammals such as elephants and hippos can also vertically mix soils down to 3 m or more (Naiman et al. 2003).

#### 15.3.2.5 Plants

Plants can also vertically redistribute P because roots collect P from soils at depth and use it to create tissue. However, P appears to be tightly conserved in desert plants, with resorption of up to 90% of the P before leaves or even woody stems are dropped. This occurs in many diverse plant genera and life forms (Lajtha 1987; Killingbeck and Whitford 2001; Charley 1977; Charley and Cowling 1968). Greater resorption appears to occur during drought stress and is greater in obligate riparian species than in facultative riparian plants and in soils with lower P availability. Resorption efficiency varies greatly among sites and years. Therefore, contribution of P to surface soils via litterfall leaching and litter decomposition is probably minimal. In addition, very low rainfall results in low leaching of P from leaves into the soil (Jobbágy and Jackson 2004). However, substantial redistribution of P can occur when roots decompose because the P found in the roots may have come from many meters away, and fine root turnover rates are high in drylands (Whitford 2002).

#### **15.4** Controls on P Bioavailability in Drylands

In dryland settings, soil P ranges from ~200 to 1,200 mg P kg<sup>-1</sup> (Turner et al. 2003a; Tiessen et al. 1984). Generally, >50% of P in dryland soils is inorganic P, in contrast to more mesic soils, which often contain a higher proportion of organic P. Dryland soils have high levels of calcium (Ca), carbonates, aluminum (Al), and iron (Fe), all of which complex with what P is present to make much of it bio-unavailable. For instance, in northern Utah, USA, 75–90% of the soil P was inorganic, mostly as Ca phosphates (80%), followed by Al phosphates (8–10%), and Fe phosphates (1–2%) (Jurinak and Griffin 1972).

Carbonate accumulation zones in dryland soils can range from 1 to 93% CaCO<sub>3</sub>, with up to 220 kg C m<sup>-2</sup>, a value similar to organic carbon in peat bogs (Monger 2006). Roots, cyanobacteria, bacteria, and other structures all contribute to pedogenic carbonate formation, along with warm, dry soil conditions (Breecker et al. 2009). Plant roots are often sheathed in amorphous or microcrystalline secondary compounds (e.g., Ca, silica) that bind P and/or form insoluble P minerals. Calcrete root coatings have up to ten times the level of P as surrounding soils (Verboom and Pate 2006). As a result, the solubility of P is mostly controlled by the sorption of P on calcite or by formation of di-calcium phosphate (Ma et al. 2009; Nadeau et al. 2007). Microbes immobilize P as well, although the levels can be quite low in dryland soils compared to mesic soils. In a Chihuahuan desert study, Lajtha and Schlesinger (1988) never found microbial biomass to be more than 3% of the total P content, even in the wet season, in contrast to peat soils where microbial biomass can be 36–55% of the total P (Walbridge 1991). Dry conditions also lead to the inactivity of microbes and enzymes and low diffusivity of soil P, and thus little degradation of organic P can occur except during pulses of soil moisture availability (Turner et al. 2003a, b).

Many studies, including those from the Great Basin, Mojave, Sonoran, and Chihuahuan deserts, USA (e.g., Schlesinger et al. 1989; Parker 1995), show P is often a limiting nutrient to dryland plants. In addition, P is needed for maximum N mineralization and nitrification (West et al. 1984). Nitrogen additions can also stimulate phosphatase activity, which is purported to increase available P (Phuyal et al. 2008; Collins et al. 2008). Soil concentrations of P, and the differential ability of plants to uptake soil P, can have a large influence on plant community composition (Midgley and van der Heyden 1999).

The positive feedback between water and nutrient uptake is especially important in dryland plants (Caldwell and Richards 1986; Radin and Eidenbock 1984). Because water is the most limiting resource in drylands (Smith and Nowak 1990), plants that are more effective at water uptake or use are likely to have a competitive advantage over other plants, including their access to nutrients. Better nutrition, including P, then facilitates the plants' capacity to acquire more nutrients and water (Caldwell and Richards 1986; Radin and Eidenbock 1984).

Wright and Mooney (1965) showed that P influences plant distributions in highpH dolomite soils, and Billings (1950) found that low P or Ca limited where sagebrush occurred in their study region. Klemmedson and Tiedemann (1998) showed a high positive correlation between available P and cover of the grass *Stipa lettermanii* (r = 0.88), whereas *Cymopterus lemmonii* was negatively correlated (r = -0.15 to -0.37) with available P. Lei and Walker (1997) showed that density of the shrub *Coleogyne ramosissima* was highly correlated with stem and foliar P (r = 0.99 and 0.80, respectively) and soil P at 7–15 cm (r = 0.68). Exotic plant species richness has also been correlated with soil available P (r = 0.84; Bashkin et al. 2003; for further discussion, see Sects. 15.4.6 and 15.5.1). Accordingly, DeLucia et al. (1989) found that *Artemisia tridentata* and *Bromus tectorum* were excluded from low-P soils. As annual plants generally have a higher nutrient demand than perennials, they are more limited by low available P than are perennial plants (Epstein 1961; Marschner 1995). Harner and Harper (1973) showed that forb cover of plant communities increases with increasing foliar P. In addition to the vascular plants described above, the species composition of lichen communities is also influenced by P levels (Bowker et al. 2006).

#### 15.4.1 Abiotic and Microbial Controls on P Bioavailability

Ultimately, the amount of biologically cycled P in dryland regions is controlled by the timing, intensity, and amount of precipitation. Soil moisture directly affects the availability of P by influencing rates of geochemical reactions, ion diffusion, and biotic activity. Because precipitation is highly variable in drylands, pulses of P-releasing activities vary on both spatial and temporal scales.

The interaction of precipitation and temperature can affect the release of bound P. The rate of  $H_2CO_3$  formation is controlled by soil water content,  $CO_2$  concentrations, and temperature (Krauskopf and Bird 1995). The solubility of carbonates and  $CO_2$  in water increases with decreasing temperature (as long as temperatures are above freezing). Thus, assuming sufficient soil moisture,  $H_2CO_3$  production should occur along spatial and temporal gradients of soil temperature. Cool, wet conditions would result in the greatest concentrations of  $H_2CO_3$ , thus decreasing soil pH, dissolving carbonates, and increasing the transition of solid-phase P to solution-phase P (Jungk and Claassen 1997). This scenario is supported by several studies. In-situ resin bags at Colorado Plateau sites showed increased soil available P during the cold, moist conditions found in winter (Miller et al. 2006a, b). Lajtha and Schlesinger (1988) also found that resin bag P peaked during cool winter conditions in the Chihuahuan desert. Magid and Nielsen (1992) showed that laboratory extractions of soils at 4°C recovered significantly more P from the soils than those done at 25°C.

The timing of rainfall relative to biotic processes is also crucial to concentrations of soil P. Precipitation that occurs when temperatures are warm results in rapid increases in microbial populations and the rate of microbial processes that affect P cycling. If precipitation occurs at the appropriate time to stimulate annual plant activity for a few weeks to months, the subsequent C inputs stimulate soil biotic activity, including processes that liberate bound P (Whitford 1999).

Most precipitation events in drylands are less than 5 mm, and thus soil surface organisms and the processes and environments they influence are able to respond to precipitation events far more often than vascular plants, because vascular plants generally require events of a larger size (depending on rooting depths) or specific seasonal timing (depending on species; Schwinning and Sala 2004). The result is a temporal decoupling between microbial and plant response to precipitation, nutrients, and carbon (Stursova et al. 2006; Belnap et al. 2004) (Fig. 15.5) and an accumulation of nutrients, including hydrolyzable organic P, and carbon at the soil surface between large rain events (Whitford 2002; White et al. 2004). Experimental addition of phosphatases showed that up to 87% of organic P in dryland soils is hydrolyzable if soils are wetted (Nadeau et al. 2007; Turner et al. 2003a).

The length of time between precipitation events and rapid soil wetting and drying influences available P in multiple ways:

- During dry periods, P accumulates on the soil surface due to high microbial mortality from desiccation and radiation damage, UV degradation of organic matter (Castenholz and Garcia-Pichel 2000), and dust accumulation (Verrecchia et al. 1995). This contributes to a flush of available P in subsurface soils when precipitation events occur.
- 2. In drylands, rewetting of dry soils and rapid drying due to high air temperatures can kill up to 58% of the soil microbial biomass (Kieft et al. 1987). The contents



**Fig. 15.5** Precipitation events are infrequent in drylands, and thus soil surfaces are most often dry. During dry times, nutrients and carbon build up on the soil surface due to dust deposition and the degradation and/or death of organisms from UV exposure. When rain occurs, most events give less than 5 mm precipitation. Whereas these small events elicit responses from surface organisms and the processes and environments they influence (including P, N, and C cycling; the death of microbes with rapid wetting/drying cycles), such low precipitation levels result in very shallow penetration of water into the soil. Thus, nutrients and carbon stay at the soil surface. Vascular plants generally require much larger events (depending on rooting depths) or specific seasonal timing (depending on species) to respond (Schwinning and Sala 2004). In addition, larger events are required to move materials such as P, N, and C to depth in the soil. Because there are many small events in between large events, substantial buildup of nutrients and carbon at the soil surface can occur. The end result is a temporal decoupling between microbial and plant response to precipitation, nutrients, and carbon

of these lysed cells, which have most of the P in the form of nucleic acids and phospholipids, can represent up to 95% of water-soluble P in Australian soils (Turner et al. 2003c) and can increase water-soluble soil P up to 1,900% (Turner and Haygarth 2001).

 Independent of microbial activity, wetting/drying cycles can increase organic P solubility by disrupting organic matter coatings and detaching and mobilizing soil colloids, leading to increased P in soil solution (Blackwell et al. 2009). However, pulses of dissolved organic P do not always occur (Butterly et al. 2009).

#### 15.4.2 Biocrust Controls on P Availability

Biocrust communities, which cover a substantial portion of dryland soil surfaces (Belnap et al. 2003c), are an especially important determinant of available P in dryland soils. As discussed above, the presence of well-developed crusts increases the capture of P-containing dust and prevents loss or redistribution of P-containing soils by wind or water. The silt and nutrient-rich clay particles captured by the crusts increase the fertility and water-holding capacity of the soil, keeping crust organisms metabolically active for a longer period of time. Biocrusts also affect available P in many other ways, as discussed below. As a result, plant uptake of P increases when plants are growing in well-developed soil crusts relative to bare sand (reviewed in Belnap et al. 2003a). For example, two sites on the same soil type in SE Utah had 82 and 81 mg P kg<sup>-1</sup> in the undisturbed, biocrusted soil versus 51 and 31 mg P kg<sup>-1</sup> in adjacent disturbed, noncrusted soils. Foliar concentrations of the shallow rooted *Festuca octoflora* at these same sites were 2.5 mg P  $g^{-1}$  soil in crusted soils versus 1.4 mg P  $g^{-1}$  soil in uncrusted soils. However, the two perennial species tested at this site showed no difference in P foliar concentrations. Before conclusions are drawn, many plant species remain to be studied.

# 15.4.2.1 Secretion of Extracellular Polysaccharides, Organic Acids, and Chelators

Most biocrust components fix C, which enters the soil 1) during the formation of polysaccharide sheaths, 2) when the organisms die (Fogg 1966; Lewin 1956) or 3) C is secreted within minutes to a few days of C acquisition. It can represent up to 50% of total fixed C and increase soil carbon by up to 300% (Fogg 1966; Lewin 1956; Rogers and Burns 1994). The increase in organic matter increases the availability of P (see Sect. 15.3.1.1). Exopolymers secreted by the crustal organisms also modulate metal-ion concentrations at the microbial cell surface. Lipid, protein, and carbohydrate components combine to create a mosaic of many polyfunctional metal-binding sites that differ in affinity and specificity. Both cations and anions, including P, can be bound (Greene and Darnall 1990). Most adsorbed metals stay on

or within the extracellular sheath and are not absorbed by the cell, thus remaining available to plants while reducing leaching losses to subsurface soils (Geesey and Jang 1990; Belnap 2003a; Verrecchia et al. 1995).

Soil crust organisms also increase available P via the excretion of H<sup>+</sup> during respiration, which decreases soil pH and frees carbonate-bound P. However, the activity of biocrust organisms can also significantly increase soil and rock pH. In SE Utah, biocrusts raised soil pH from ~8 to ~10.5 (Garcia-Pichel and Belnap 1996), and endolithic cyanobacteria in Venezuela and South Africa raised the pH from ~8 to ~10 (Büdel 2000).

Many biocrust organisms secrete organic acids such as citrate, malate, acetate, pyruvate, lactate, formate, and fumerate (Belnap 2003b; Whitton et al. 2005). Specific lichen-secreted organic acids include physodate, lobarate, salzinate, stictate, evernate, lecanorate, roccelate, atranorate, norstictate, oxalate, and usnate acids. All these compounds can solubilize bound P (see Jones and Oburger 2011; Jones and Wilson 1985). What compounds are released is often specific to a particular species or genera. For instance, mat-forming ectomycorrhizae in dryland riparian areas secrete oxalate, but the common upland mycorrhizal species *Glomus* and *Acaulospora* do not (Allen et al. 1996). Whereas the fungus *Aspergillus niger* and the bacterium *Penicillium simplicissiumum* produce citrate, many other species of fungi and bacteria cannot solubilize bound P (Barroso and Nahas 2005). Fungi can also secrete acids within rocks, penetrating to depths of up to 4 m (Bornyasz et al. 2005), solubilizing nutrients and transferring these nutrients, including P, directly to plant roots (Van Breemen et al. 2000).

Biocrust organisms also secrete powerful metal chelators, such as siderochromes, that increase available P by maintaining metals in solution (Lange 1974; McLean and Beveridge 1990; Schelske et al. 1962; Belnap 2003b). Cyanobacteria also secrete peptide N and riboflavin. Together with other chelators, these substances form complexes with tricalcium phosphate, copper, zinc, nickel, and ferric iron, keeping the nutrients plant-available. Because chelators are watersoluble, these nutrients are also available to associated nonchelating plants or microbes (Lange 1974; Geesey and Jang 1990; Gadd et al. 2007). Soil cyanobacteria also secrete glycollate, which stimulates phosphate uptake (Fogg 1966).

#### 15.4.2.2 Secretion of Phosphatases

Most soil and hypolithic cyanobacteria, green algae, lichens, and mosses have phosphatases in their cell walls and mucilaginous sheaths. Most of the cyanobacteria and fungi tested release extracellular phosphatases into the surrounding soil. Phosphatases hydrolyze organic phosphates, liberating P (Turner et al. 2003b; Nannipieri et al. 2011). Once released, these compounds can then be immobilized by microbes, transferred to plant host roots, or stabilized by humic substances (Sinsabaugh 1994; Lindahl et al. 2005). Phosphatase activity was found to be higher under well-developed biocrusts than under nearby bare soil (Bolton et al. 1993). However, as phosphatase is highly correlated with soil organic matter and

organic matter is relatively low in dryland soils, phosphatase activity is expected to be relatively low in drylands relative to more mesic ecosystems (Sinsabaugh et al. 2008).

The expression of phosphatase is somewhat inducible. As Whitton et al. (2005) discuss, whereas P in the medium induces phosphatase activity in small unicellular organisms (e.g., bacteria), larger multicellular cyanobacteria appear instead to respond to internal P concentrations. Phosphatase activity can also be inhibited by P-binding metal ions (e.g., zinc, iron, manganese). Temperature optima appear to vary with species and phosphatase form. For instance, Nostoc commune UTEX 584 shows optima of  $32^{\circ}$ C for phosphomonoesterase and  $42^{\circ}$ C for phosphodiesterase. There also is light sensitivity in this species, with activity consistently highest in the dark, followed by activity in low and then in high light. Phosphatase activity in cyanobacteria increased with increasing Ca and decreased with magnesium, whereas potassium and sodium had little effect. Dried Nostoc samples show phosphatase activity even after many months or after organisms die or are removed. Phosphatase activity can be increased in soil by up to 27% by adding extracellular polysaccharides from cyanobacteria without the living organisms being present (de Caire et al. 2000). Free-living and lichenized cyanobacteria also fix N. When soil N is elevated, phosphatase amount and activity also increases, as discussed in Sect. 15.4 (Collins et al. 2008; Phuyal et al. 2008), increasing labile (resin- and bicarbonate-extractable) soil P as well (Zou et al. 1995).

In environments with low or highly variable levels of P, such as dryland soils, phosphatase-coated, multicellular hairs are found in cyanobacteria and sometimes green algae (Whitton et al. 2005). These hairs have long tapered ends that are highly vacuolated, providing a high surface area for P absorption. In colony-forming cyanobacteria, these hairs can extend out beyond the colony. Smaller hairs are also formed in response to Fe and N limitation, but do not show phosphatase activity. It is not known if the hairs can be used to access inorganic P.

#### 15.4.3 Fungi as Connectors

Biocrust fungi and subsurface fungi are clearly crucial in P cycling in drylands. Most desert plants are mycorrhizal (Whitford 2002), a relationship that is well-known to increase P uptake and tissue concentration in vascular plants (see Jansa et al. 2011). Strong positive correlations have been shown between mycorrhizal infections of desert seed plants and biocrusted surfaces, as plants in biocrusted soils from SE Utah have up to three times higher mycorrhizal infection rates in crusts compared to plants in bare soil (reviewed in Belnap et al. 2003a). However, mycorrhizal abundance decreases with aridity as they are replaced with proportionally more dark septate ascomycetes in dryland soils (Green et al. 2008). These dark septate fungi form endophytic and ectophytic associations with plants, nondestructively colonizing the root cortex and surface, shoot and stem surfaces (including the inside of hairs), and the vascular cylinder (Barrow and Osuna 2002). The same

species found on roots can be found free-living in the soils. These organisms can solubilize rock phosphate and tricalcium phosphate and have been shown to increase P in roots and shoots in the sedge *Carex*, the grass *Vulpia ciliate*, and the shrub *Atriplex canescens* (Mandyam and Jumpponen 2005). Fungal networks, dominated by dark septate fungi, transfer C and N (and probably P as well, although it was not measured in this experiment) up to 100 cm per day between plants and cyanobacterial biocrusts (Green et al. 2008).

#### 15.4.4 Soil Fauna Controls on P Availability

In drylands, soil microfauna have greater abundance, activity, and richness under well-developed biocrusts than under less well-crusted soils (Belnap 2003b; Darby et al. 2007). The selective feeding of soil microfauna on microbes affects factors that influence P cycling, including microbial abundance and community composition, microbial enzyme production, and release of P when the microbes are eaten (Bardgett 2005). Multiple studies show that the nutrients released by the death of microorganisms are utilized by plants (as discussed in Bardgett 2005). Soil microfauna and macrofauna also fragment litter, increasing decomposition rates that indirectly increase available P. Because populations vary seasonally, the release of microbial P will vary seasonally as well. However, as discussed in Sect. 15.3.2, the importance of soil fauna in P cycling varies widely among different dryland regions.

#### 15.4.5 Plant Controls on Soil P

Plants utilize multiple mechanisms to increase their access to soil P in all environments, as discussed by George et al. (2011). In dryland regions, some of these mechanisms are employed more often than others, as discussed below.

First, alteration of key root characteristics can increase plant P uptake. Plants with higher root cation exchange capacities (CEC) can more readily access recalcitrant P (Drake and Steckel 1995), and as dicotyledonous plants generally have higher root CECs than monocotyledonous plants, they should be favored in P-limited soils (Marschner 1995). This may partially explain why dicotyledonous plants heavily dominate dryland regions. Roots generally contact only 0.5% of dryland soil volume at any one time (Lynch and Deikman 1998) and thus an increase in this contact is probably advantageous for P uptake. Most dryland plants utilize fungi to enhance their ability to exploit the soil volume (Lajtha and Harrison 1995; Gadd et al. 2007; Quiquampoix and Mousain 2005; also see Sect. 15.4). Although root uptake capacities could theoretically be increased, P uptake is probably more limited by low soil diffusion rates than root uptake capacity (Lajtha and Harrison 1995; Clarkson 1985). In addition, some plants such as *Larrea* 

actively maintain space around their roots via root exudates (root exclusion), whereas others such as *Ambrosia* utilize a root-recognition response to maintain space (Schenk et al. 1999). Root segregation in dryland soils allows plants to dominate belowground space, giving increased access to nutrients, especially immobile nutrients such as P, and thus promoting the plant's competitive ability (Casper and Jackson 1997). The root-recognition response appears more effective at accessing soil P because root self-incompatibility may limit flexibility in exploring the soil volume (Caldwell and Richards 1986).

A second way by which plants affect soil available P is through hydraulic redistribution, which is exudation of water by roots into dry soil pockets (Caldwell and Richards 1986). This is a common phenomenon in dryland plants. The exuded water enhances soil available P and both the water and nutrients are available for re-uptake. Third, dryland plants also have P-conserving strategies. Woody shrubs and evergreen life forms with long-lived tissue dominate these regions. As discussed in Sect. 15.3.2.5, large amounts of P are also resorbed in these plants before tissue is dropped. Both these mechanisms reduce the need for additional P uptake to construct new tissue (Jonasson and Chapin 1991).

Fourth, the most common way for plants to access bound P in dryland soils is to acidify the rhizosphere via release of H or OH/HCO<sub>3</sub> to counterbalance net excess of cations or anions, and all dryland shrubs tested showed a decrease in rhizosphere pH relative to bulk soil (Ma et al. 2009). Fifth, plant roots can also exude a wide range of complex mixtures of organic acids (e.g., oxalate, malate, succinate), phytosiderophores, sugars, vitamins, amino acids, purines, nucleosides, inorganic ions, gaseous molecules, a wide array of chelators, enzymes such as phosphatases and phytases, root border cells, and phospholipid root surfactants, all of which can act to make bound P bioavailable (Callaway 2007; Jurinak et al. 1986; Ouiquampoix and Mousain 2005). The secretion of many of these compounds can be enhanced or suppressed, depending on soil concentrations of P. In addition, as with cyanobacteria, plant phosphatase and phytase activity can be inhibited by polyvalent anions such as phosphate and some forms of P-binding metal ions (zinc, iron, manganese). Plant phosphatases are also secreted in response to water stress and salinity, with drier sites showing much higher soil and shrub root surface phosphatase activity than more mesic sites (Sardans et al. 2006; Estiarte et al. 2008; Li and Sarah 2003). Various plant species, and litter from these plants, have differential effects on stimulation of soil phosphatase and thus on P availability (Dornbush 2007).

A sixth way by which plants can influence available P is via leaching of leaves or litter. In drylands and seasonally dry areas of the world, plant leaves of the *Casuarinaceae* and *Proteaceae* contain carboxylicates and hydroxylic acids that free bound P (Verboom and Pate 2006). Over 200 families of angiosperms and gymnosperms, representing 74% of the angiosperm families, contain oxalate in their tissues. Oxalate also occurs in the wood of more than 1,000 species and some cacti contain up to 80% dry weight calcium oxalate (Horner and Wagner 1995). Many exotic plant invaders secrete compounds to access recalcitrant P (for further discussion, see Sect. 15.4.6). In the Karoo Desert of South Africa, many plant

leaves contain malate, citrate, and oxalate which, upon leaching, increase soil available P (Whitford 1999). Because most of these compounds are water-soluble, exudates from one plant can benefit neighboring plants and microbes. This has been shown in agricultural systems: the P-releasing activity of *Vicia faba* facilitates P uptake in *Zea mays*, and the P-releasing activities of *Cicer arietinum* facilitate P uptake by *Triticum aestivum* (Zhang and Li 2003). The presence of the invasive plants *Bromus tectorum*, *Halegeton glomeratus*, *Salsola* spp., and *Centaurea maculosum* in the western USA have all been shown to facilitate P availability for neighboring native plants (Allen and Allen 1988; Fox and Comerford 1990; Herron et al. 2001; Thorpe et al. 2006; Belnap and Sherrod 2009).

Lastly, N-fixing plants have higher tissue levels of N than nonfixing plants and thus their tissue often decomposes quickly, releasing P (Naiman et al. 2003). As discussed above in this section, high soil N can also elevate phosphatase activity and thus soil available P. This can be an amplifying feedback because fertilization with P often increases N as well (Reed et al. 2007).

There are also amplifying feedbacks between soils and plants in dryland ecosystems that affect soil available P. Large woody plants of dryland ecosystems and the microorganisms associated with them often alter soils to optimize the capture and utilization of limiting water and nutrients, including P, which in turn alters plant community composition (Verboom and Pate 2006). However, the strategies to increase the availability of P in soils can be quite costly in terms of plant carbon (Lynch and Ho 2005; DeLucia et al. 1997; James et al. 2005). Because dryland plants are already water and nutrient limited and thus carbon is scarce, the cost of making P bioavailable may be much more challenging than for plants growing in more mesic regions (James et al. 2005). For example, root exudates have been estimated to represent up to 50% of all belowground carbon allocation, up to 25% of photosynthetic production, and up to 20% of total plant dry weight (James et al. 2005). Because available P is very low in dryland soils, the proportion of carbon allocated to P uptake is likely to be even higher in these plants. Mycorrhizal associations also cost the infected plant carbon, which can range from 4 to 20% of daily net photosynthesis (James et al. 2005). In addition, the need for soil moisture may place temporal restrictions on when such mechanisms can be employed, as they may be possible only during rainy seasons or in years with above-average precipitation.

#### 15.4.6 Interactions Between Invasive Plants and P Availability

Scientists have long attempted to understand what plant properties allow particular species to become highly invasive (e.g., Lonsdale 1999). In the low available P soils of the drylands of western USA, the most pervasive and threatening invasive species include *Centaurea diffusa*, *C. maculosa*, *Halogeton glomeratus*, *Salsola* spp., *Lepidium latifolium*, *Bromus tectorum*, *B. madretensis*, *Schismus barbatus*,

and *Taeniatherum caput-medusae*. The success of these plants is at least partially due to their ability to (1) access nonbioavailable P more efficiently than native plants, (2) outcompete native plants for soil P, and/or (3) be more efficient in P uptake or utilization than native plants. The strategies used are those listed in Sect. 15.4.5, including root exudates and leachates of aboveground tissue that contain organic acids, more efficient P uptake and/or utilization, and being overall better competitors when P is not limiting to the invasive plants (Table 15.1). The distribution of some of these species is also significantly correlated with soil available P. Many invasive plants in dryland ecosystems are early successional annual species, colonizing areas with few other plants or fungi to assist in P uptake. Thus, the ability of these species to develop means of accessing relatively unavailable P in such situations may have, at least partially, led to their superior competiveness.

## **15.5** Case Study: Interaction Between Exotic Annual Grasses and Soil P Availability in the Western United States

#### 15.5.1 Controls of P on Exotic Annual Plant Distribution

How soil physical and chemical characteristics influence the cover of *B. tectorum*, B. madretensis, and S. barbatus has been investigated by the Belnap laboratory (unpublished results). We used maps of soils, geology, topography, and geologic surfaces (delineating the age and composition of the soil surface) to identify sites representing a broad range of soil texture, chemistry, and elevation within four of the six US deserts: Chihuahuan, Mojave, Colorado Plateau, and the Great Basin (we did not sample the Sonoran or Columbia Plateau). Climate maps were then used to sample these representative conditions across a gradient of temperature and rainfall timing and amount (hot Chihuahuan Desert with relatively high amounts of summer-dominant rainfall; hot Mojave Desert with low amounts of winter-dominant rainfall; cool Colorado Plateau Desert with higher amounts of summer/winter mixed rainfall; cool Great Basin Desert with high amounts of winter-dominant rainfall). Within each selected unit, we sampled 0-10 cm soils in adjacent invaded and uninvaded patches (Fig. 15.6). In the Chihuahuan Desert, where no annual grass patches were found, we sampled the approximate center of the desired soil type as outlined on the soil survey.

Our results suggest that as the ratio of cool season to total precipitation increases, as well as the total amount of cold season precipitation, so do conditions that allow the conversion of bound P into bioavailable P (Fig. 15.7). In the hot Chihuahuan Desert, where the percentage and total amount of winter rainfall is very low, we found no annual grasses at our sites. Our hypothesis is that soils are seldom cool and wet in this desert, and thus soil P remains bio-unavailable. In the hot Mojave Desert, where total winter rainfall is higher than in the Chihuahuan but still low compared

Table 15.1 The me	pre problem	atic exotic in	wasive plants	in US dryland	I regions and th	e ways in which	they affect soil P availability
Plant	Root	Tissue	Better	Uptake	Utilization	Distribution	References
	exudates	leachates	competitor	efficiency	efficiency	control	
Centaurea diffusa	×		×	×			Callaway (2007), LeJeune and Seastedt (2001),
							LeJeune et al. (2006), Suding et al. (2004),
							Callaway and Aschehoug (2000)
Centaurea				×	×		Harvey and Nowierski (1989), Herron et al. (2001),
maculosa							Thorpe et al. (2006)
Halogeton		×					Allen and Allen (1988), Cook and Gates (1960),
glomeratus							Duda et al. (2003)
Salsola spp.		×					Allen and Allen (1988), Cannon et al. (1995), Fox
:							and Comerford (1990)
Lepidium latifolium	×						Blank and Young (2002)
Bromus tectorum	×					×	Belnap unpublished results
Bromus						×	Belnap unpublished results, Yoder and
madretensis							Nowak (2000)
Schismus barbatus						×	Belnap unpublished results
Taeniatherum	×					×	Blank and Sforza (2007)
caput-medusae							
v indicates a mositiv	ie effert						

× indicates a positive effect



Fig. 15.6 An illustration of the patchy nature of *Bromus tectorum* invasion in many parts of the western USA (*arrows* mark the *light-colored Bromus* patches)



**Fig. 15.7** Conceptual model of the relationship between climate and soil factors (nutrients and water) controlling annual grass distribution in the different US deserts. Limiting nutrients are listed in order of importance within regional boundaries. The *numbers* within the regional boundaries indicate the average annual amount of precipitation (mm) when air temperatures are below  $10^{\circ}$ C relative to total precipitation. We suggest that as this ratio and the total amount of cool season precipitation increase, so do conditions that allow the conversion of bound P into bioavailable P. As P becomes less limiting, other cations become more important to annual grass distribution. Although we do not have data (*ND*) on the limiting soil factors in the Sonoran desert, soils are expected to show strong P limitation. We found no (*slashed O*) annual grasses in the Chihuahuan desert

to other deserts, available P has strong control over annual plant distribution ( $r^2 = 0.83$ ). On the Colorado Plateau, available P becomes less limiting when soils are cool and wet, especially at lower elevation (1,400–1,585 m elevation,  $r^2 = 0.29$ ; >1,585 m elevation,  $r^2 = 0.63$ ), and other cations (potassium and magnesium) and water become more important to annual grass establishment. In the Great Basin, with an even greater time of cool, wet soils, P does not appear to affect annual grass distribution. Although we do not have data on the limiting soil factors in the Sonoran Desert, our hypothesis would suggest that soils will be strongly P-limited, and annual grasses thus controlled by available P.

#### 15.5.2 The Interaction of Soil P and Bromus tectorum

Bromus tectorum is an annual grass that currently dominates vast regions of the western USA, and many studies have been done on how soil nutrients affect this species. In SE Utah, USA, field measurements showed that resin-extractable P best predicted relative growth rates of *B. tectorum* in fall (r = 0.40 in watered and 0.59 in unwatered plots) and winter (r = 0.53 in watered and r = 0.65 in unwatered plots) (Miller et al. 2006a, b). Other soil factors best predicted germination, and spring and overall growth rates, indicating that resource needs shifted with season and soil moisture, similar to the regional scale resource limitations discussed above. In these soils, although available P levels were above those considered "critical" for plant growth, they were still below those considered adequate for unrestrained plant growth. In another study, *B. tectorum* again showed high levels of winter root growth when soils were cold and moist (Harris 1967).

Other studies show that *B. tectorum* can be P-limited. Belnap et al. (2003b) showed that *B. tectorum* germination was suppressed when available P was reduced. DeLucia et al. (1989) found that *B. tectorum* biomass was reduced by over 90% when growing on P-limited soils. Gundale et al. (2008) also found *B. tectorum* growth was limited by low soil P. Bashkin et al. (2003) found a landscape-level correlation between *B. tectorum* biomass and available P.

Nitrogen deposition has been thought to also play a role in annual grass invasions (Fenn et al. 2003), although it may be via an indirect effect on available P. Multiple studies have shown that N additions stimulate phosphatase activity, thus probably increasing available P (Phuyal et al. 2008; Collins et al. 2008).

There are multiple lines of evidence showing that *B. tectorum* can convert recalcitrant P to labile forms. A patchy invasion of *B. tectorum* into a never-grazed (by livestock) grassland showed that labile P was much higher in invaded plots than in adjacent uninvaded plots at the same site (45.6 vs. 14.6 µg P g<sup>-1</sup> soil, respectively) (Hansen 1999) whereas there were no significant differences in soil available P before the invasion (Kleiner and Harper 1977). In addition, the higher the *B. tectorum* cover, the higher the increase in labile P; as *B. tectorum* cover increased from 0 to 10 to >40% cover, labile P increased from 14.6 to 19.5 to 28.2 µg P g<sup>-1</sup> soil.

Miller et al. (2006a, b) also found greater available P in plots with *B. tectorum* compared to those without *B. tectorum*.

Similar results have been obtained from plots in SE Utah at various locations (Belnap and Robert Sanford Jr, University of Denver unpublished results). In a 30-month study where plots were sampled monthly, native plant plots (dominated either by the perennial  $C_4$  grass *Hilaria jamesii* or the perennial  $C_3$  grasses *Stipa hymenoides* and *S. comata*) that had been invaded by *B. tectorum* had higher resinextractable and labile P than adjacent native-only plots. Similarly, a 12-month study (Fig. 15.8) at another site again showed resin-extractable and labile P higher in *Stipa* plots invaded by *B. tectorum* than in native-only plots. This difference was most pronounced in June when all plants were dormant, and in October when native grasses were dormant and *B. tectorum* was in the seedling stage.

In the same never-grazed grassland as the Hansen (1999) and the 30-month labile P studies, Belnap and colleagues (unpublished results) also sampled available P annually in the spring from 1995 to 2006 (Fig. 15.9). As seen at the other study sites, *Stipa–B. tectorum* plots showed elevated available P at over half of the sample



**Fig. 15.8** Monthly measures (Jan – Dec 2002) of bioavailable P in a grassland grazed for over 100 years outside Canyonlands National Park in SE Utah, USA. Samples were taken from adjacent invaded and uninvaded sites where the dominant native is the  $C_3$  grass *Stipa hymenoides. Upper panel*: resin extractable P. *Lower panel*: labile P (resin- and bicarbonate-extractable total P). Note that resin-extractable and labile P concentrations are almost always elevated in the invaded sites relative to the uninvaded sites, especially in June when all plants are dormant, and in October, when natives are dormant (Belnap and Sanford unpublished results)



**Fig. 15.9** Annual spring measures (May 1996–Apr 2006) of bicarbonate-extractable (available P) in a grassland never grazed by livestock (Canyonlands National Park) in SE Utah, USA. *Upper panel*: available P in adjacent invaded and uninvaded sites where the dominant native is the  $C_4$  grass *Hilaria jamesii*. *Middle panel*: available P in invaded and uninvaded sites where the dominant native is the  $C_3$  grass *Stipa hymenoides*. Note that when available P is significantly different between invaded and uninvaded sites, it is most often higher in the invaded sites, especially in the *S. hymenoides* communities (Belnap and colleagues unpublished results). *Lower panel*: Total precipitation received in the 6 months prior to the available P sampling. There is a high correlation between available P and total precipitation received in the 6 months prior to sampling (Belnap and colleagues unpublished results)

times relative to *Stipa*-only plots, whereas the results in the *H. jamesii–B. tectorum* versus *H. jamesii*-only plots were more mixed. Levels of available P were highly correlated with total precipitation that occurred in the 6 months prior to the sampling time (*H. jamesii* dominated plots, r = 0.49; *H. jamesii* with *B. tectorum* 

plots, r = 0.55; *Stipa* plots, r = 0.62; *Stipa* with *B. tectorum* plots, r = 0.56). This is similar to the observations of Miller et al. (2006a, b) that greater precipitation results in greater available P in soils dominated by *B. tectorum*.

In the greenhouse, where pots were watered and thus soil moisture was relatively high, P fractions in four different soil types (high and low sand, high and low CaCO<sub>3</sub>) were analyzed before and after planting with *B. tectorum* (Fig. 15.10) (Sanford and Belnap unpublished results). Soils before planting and those in control pots (watered, no *B. tectorum*) showed very high percentages of HCl-extractable P, whereas soils with *B. tectorum* present for 100 days had almost no HCl-extractable P remaining, indicating that *B. tectorum* had facilitated the conversion of almost all the recalcitrant P to bioavailable P.

All these lines of evidence indicate that *B. tectorum* is able to access P that is otherwise unavailable to native plants. This is most likely via root exudates, as the greenhouse studies did not allow for plant litter or leaf leachates to influence soil P (there was no litter, and plants were not watered from above). This hypothesis is also supported by the correlation between the increase in available P and precipitation (either in the field or the greenhouse), because increased soil moisture would be present at the time when *B. tectorum* would have more carbon available to produce root exudates.



**Fig. 15.10** Changes in HCl-extractable (recalcitrant) P for each of four soils (**a–d**), representing high and low sand and CaCO<sub>3</sub> values. *Pre* indicates measurements from soils before they were planted with *Bromus tectorum*. *Control* indicates measurements from soils that had water added but were not planted with *B. tectorum*. *B. tectorum* measurements are from soils where *B. tectorum* was planted, watered, and grown for 100 days. *Bars* indicate one standard deviation. Note the almost total conversion of the highly recalcitrant P in *B. tectorum* pots to more labile forms of P. Pre and Control samples were not significantly different from each other, whereas the *B. tectorum* treatment was different from both of them in all soil types (\**P* <0.05) (Belnap and Sanford unpublished results)

## 15.6 Climate Change Effects on Biological P Cycling in Drylands

Because climate change is expected to affect both temperature and precipitation in dryland regions and both of these factors have a strong influence on the availability of P through both direct and indirect mechanisms, changes in climate will have a substantial impact on P cycling in drylands. As discussed above, the interaction of these two factors can directly affect concentrations of available P in soils. Plants whose distributions are limited by available P will probably see habitats shift in space. For instance, as temperatures increase and soil P becomes less available (due to loss of wet, cool conditions), we might expect the invasive annual grasses found in the western USA to expand their range into more northern habitats, such as the Colorado Plateau, while disappearing from parts of the southern Mojave desert. In regions where temperatures are predicted to rise but precipitation to stay the same or decrease, such as the western USA, a decline in soil moisture will result. This, in turn, will lead to a reduction in biological cycling of P in dryland soils due to multiple factors:

- 1. A decline in soil moisture will slow all abiotic processes that release biounavailable P because these processes depend on soils being moist.
- 2. Whereas increased temperature could increase microbial activity, reduced soil moisture will limit activity time and probably lead to a decrease in microbial abundance and activity (Sardans et al. 2006). This will reduce acidification via respiratory activities and the production/excretion of enzymes, chelators, and other compounds that release bound P. In addition, the expected reduction in plant biomass, including root biomass, will result in a further reduction of soil acidification and root exudates that release bound P (DeLucia et al. 1997; Li and Sarah 2003).
- 3. Reduced precipitation will slow litter decomposition. Less soil water may also increase the production of more recalcitrant litter (e.g., more wax on leaves to reduce water loss), further slowing decomposition rates.
- 4. The activity of many compounds, such as phosphatases, is more dependent on soil water availability than substrate availability and thus their effectiveness will be reduced (Sardans et al. 2008).
- 5. Fewer wetting/drying events will result in less P being released from dying microbes or from physical processes that release P.
- Greater N deposition will increase P uptake and thus increase P limitation in many ecosystems (Aerts and Bobbink 1999; Phuyal et al. 2008).
- 7. Drought and warming will increase plant resorption of P, resulting in less P in litter (Killingbeck and Whitford 1996; Sardans et al. 2006).
- 8. If soil surfaces are disturbed, the expected decrease in plant biomass will lead to higher sediment movement, and thus an accelerated loss of soil P via wind and water erosion.

However, there will be some factors offsetting these expected declines in soil available P concentrations in dryland regions. Multiple factors will also reduce P

uptake, such as reduced microbial and plant biomass, soil moisture, diffusion of P to roots, and root P uptake (Bradford and Hsiao 1982). Increased N deposition is also likely to stimulate the release of bound P.

## 15.7 Conclusion

There are many factors that distinguish biological P cycling in drylands from P cycling in more mesic regions (Table 15.2). In drylands, P inputs and losses are due more to the deposition and loss of dust than to factors such as weathering and downward leaching. In these sparsely vegetated landscapes, the redistribution of P is a major driving force in determining soil P levels and thus plant and animal community structure. In addition, concentration of P at the soil surface leaves these ecosystems highly vulnerable to loss of P via wind and water erosion. In these landscapes, the high pH and the abundance of CaCO<sub>3</sub> and other compounds in soils that complex with P result in low bioavailability. Although microbes and plants have many varied mechanisms to free bound P. low rainfall in these regions limits both the biomass of these organisms and the efficacy of these strategies, while also conferring a proportionally high carbon cost. Many of the more successful invasive plants in dryland regions are those able to access recalcitrant P more effectively than native plants. Because P availability is ultimately dependent on soil moisture and temperature, climate change is expected to have large impacts on P cycling in dryland regions.

Aspect of P cycling	Drylands	Mesic areas
P redistribution	High	Low
Hours of dry soils	High	Low
Size and frequency of plant gaps	High	Low
Number of intense rain events	High	Low
Distance to free surface water	High	Low
Horizontal distribution	High	Low
Animal vertical mixing	Low	High
Plant vertical mixing	Low	High
P availability	Low	High
Inorganic P	High	Low
P complexed with CaCO <sub>3</sub>	High	Low
Organic matter	Low	High
Microbial immobilization	Low	High
Soil diffusivity	Low	High
Decomposition rates	Low	High
Times of soil moisture	Low	High
Phosphatase release/activity	Low/high	High/low
Root exudates	Low	High
Carbon for mycorrhizae	Low	High

Table 15.2 Comparison of different aspects of P cycling between drylands and more mesic areas

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