Mechanisms Determining Patterns of Nutrient Dynamics

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Nutrient availability is a critical controller of plant species composition and productivity and is influenced by the interaction of a number of biotic and abiotic factors (Chapin et al. 2002). In this chapter, we explore the controls over nutrient pools and fluxes across different California grassland types. We will begin with an in-depth discussion of the exotic-dominated annual grassland type, where most biogeochemical studies have occurred. Patterns in these annual grasslands will then be compared to those in native grasslands and oak-grassland matrices. Finally, we will review the roles of organisms other than plants in influencing nutrient dynamics.

General Patterns of Nitrogen Pools and Fluxes in California Annual Grasslands

Most nutrient studies in California grasslands have focused on nitrogen (N), probably because it is the most common limiting nutrient to plant productivity in these grasslands (Hoglund et al. 1952; Woolfolk and Duncan 1962; Jones 1963; Harpole et al., Chapter 10). The relatively few comprehensive nitrogen budgets in California grasslands (Jones and Woodmansee 1979; Jackson et al. 1988; Center et al. 1989) report a wide range of N pools (Table 8.1) and fluxes (Table 8.2) within and across studies, but they also highlight some strong consistent trends (Table 8.1). Most N is stored as soil organic N (concentrated in the top 4 cm of the soil profile), with less than 10% of ecosystem N in plant and microbial biomass at peak standing plant biomass in May (Jones and Woodmansee 1979; Jackson et al. 1988; Herman et al. 2003). The top 10 cm of soil contain 85% of live root biomass N and 75% of microbial biomass N (Jackson et al. 1988; Jackson et al. 1989), with most of that within the top 1–5 cm (Evans et al. 1975; Woodmansee and Duncan 1980). The distribution of plant N in belowground vs. aboveground tissues has been estimated to range between 0.9:1 and 1.33:1 (Jackson et al. 1988; Center et al. 1989) (Table 8.1).

Nitrogen inputs and outputs are highly variable across years and sites (Table 8.2). Inputs through biological N fixation largely depend on the prevalence of legumes, although inputs of 0.18–12 kg N/ha/yr can be seen even in grass-dominated sites (Table 8.2). There is a lack of comprehensive data on total atmospheric N deposition because most measurements of N deposition do not include all sources of wet, dry, and fog deposition (Fenn et al. 2003b). Measured inputs of atmospheric deposition into most grassland sites are less than 2 kg N/ha/year (Jones and Woodmansee 1979; Center et al. 1989; Takemoto et al. 1995; Air Resources Board 1995), but modeling studies estimate that total deposition is more likely to range from 4–7 kg N/ha/year in most grassland sites, with higher levels (9–12 kg N/ha/year) in some parts of Southern California (Fenn et al. 2003b).

Nitrogen losses can occur through leaching, gaseous loss, and soil erosion. Estimates of N losses through leaching range from 0.18–63 kg N/ha/year, with high year to year variability. Typical leaching rates of grass-dominated sites are at the far low end of this range; the high estimates come from systems dominated by legumes and from studies using tank lysimeters (Jones and Woodmansee 1979; Davidson et al. 1990; Maron and Jeffries 2001). Most studies from intact grasslands measure N leaching in the range of 1–4 kg N/ha/year. The most comprehensive study on N leaching in California grasslands demonstrated that, over 20 years, mean NH_4^+ leaching was less than 0.1 kg N/ha/yr, while NO_3^- leaching averaged 1.59 kg N/ha/yr, and ranged from 0.18 to 3.6 kg N/ha/yr (Lewis et al. 2006). Few studies have closely followed leaching of dissolved organic N (DON), but at some time points, up to 87% of leached N can be in the form of DON (S. Parker, personal communication), suggesting that N leaching may be greatly underestimated in these grasslands if only NO_3^- or NH_4^+ are measured. Annual estimates of N gas loss are, to our knowledge, unknown, but peak seasonal instantaneous rates range from less than 1 to 13 ng/cm²/hr

TABLE 8.1
Range of Pools of N (kg N/ha) at Peak Standing Biomass in the Spring in Grass-Dominated Sites

Pool	Pool size (kg N/ha)
Aboveground live plant	33–80
Aboveground litter	11–28
Live roots	20–80
Dead roots	17–29
Soil microbial biomass	10–133
Available N	1–44
Soil organic N	2,000–6,000

NOTE: Values based on Jones and Woodmansee 1979, Woodmansee and Duncan 1980, Jackson et al. 1988, Center et al. 1989, Dahlgren et al. 1997.

TABLE 8.2
Range of Fluxes of N (kg N/ha/yr)

Flux	Flux (kg N/ha/yr)
N fixation, grass-dominated	0.5–12
N fixation, legume-dominated	50–200
Atmospheric deposition	<1–17.8 (most estimates range from <2.0 to 7)
N release through aboveground litter decomposition	47–71
N release through root litter decomposition	32–65
N release through seeding thinning	40–104
Net N mineralization	57–125
Total plant N uptake	68–119
N leaching	0.18–13 (most sites 1–3)[a]
N sediment loss[b]	0.044–0.91 (20 year average of 0.38)
N gas loss	No annual loss numbers available, but rates at fall wet-up range from <1–13 ng/cm^2/hr

NOTE: Values based on Shock et al. 1984, Vaughn et al. 1986, Davidson et al. 1990, Hart et al. 1993, Takemoto et al. 1995, Air Resources Board 1995, Fenn et al. 2003, and unpublished data

[a]Tank lysimeter studies report as high as 63, but likely overestimate.

[b]N sediment loss estimate based on 20 year sediment export data (Lewis et al. 2006) at the Sierra Foothills Station (Yuba County), along with measurements of soil %N from this site (Davidson et al. 1990).

(0.0001–0.0013 kg N/ha/hour) (Hungate et al. 1997c; Herman et al. 2003), and likely do not significantly contribute to annual N loss (Herman et al. 2003).

Nitrogen inputs and outputs are usually small compared to internal N cycling rates (Table 8.2). Nitrogen turnover is rapid in annual-dominated systems, with particularly large seasonal changes in plant and litter N pools (Jackson et al. 1988; Jackson et al. 1989; Davidson et al. 1990). At senescence, 63–77% of aboveground plant nitrogen is translocated to seeds, and only 23–37% remains in the aboveground litter, while N does not appear to be retranslocated from senescing roots (Woodmansee and Duncan 1980; V. T. Eviner and C. E. Vaughn personal communication). Root litter tends to fully decompose within one year (Savelle 1977; V. T. Eviner, personal observation), while it takes roughly 2.5 years for aboveground litter to decompose completely (Heady et al. 1991), with loss of 59–79% of aboveground litter mass within the first year (Savelle 1977; Jones and Woodmansee 1979). Litter N loss does not necessarily follow the pattern of litter mass loss (Dukes and Field 2000) because decomposing litter frequently accumulates N (Center et al. 1989; Hart et al. 1993). Some studies have shown nearly complete turnover of litter N within a season (Jackson et al. 1988), while others show virtually no litter N loss despite large litter C and mass losses (Henry et al. 2005).

Nitrogen budgets of California annual grasslands have indicated that decomposition and N fixation often cannot meet plant demands for N, suggesting that N is made available from seedling thinning throughout the growing season (Woodmansee and Duncan 1980; Pendelton et al. 1983; Vaughn et al. 1986; Center et al. 1989; Heady et al. 1991). As mentioned above, about 70% of aboveground N is in seeds at the time of plant senescence. On average, there are 60,000 germinable seeds per m^2 at the start of the growing season (Bartolome 1979), with the number reaching as high as 300,000 (Young et al. 1981). Over 90% of these seeds germinate shortly after the first significant rainfall, but within the first seven weeks of the growing season, 50–75% of these seedlings die (Bartolome 1979, Young et al. 1981). These are

very young seedlings containing almost no structural compounds and thus are a substantial source of labile carbon and nutrients, leading to an early season N pulse that exceeds the total N content of aboveground litter (V. T. Eviner and C. E. Vaughn, personal communication). Despite the death of half of the seedlings within the first two months of the growing season, seedling density is high at the onset of winter, at 20,000–40,000 individuals per m^2. Thinning continues through the growing season, resulting in 8,000–20,000 individuals per m^2 by the end of the growing season in late spring (Heady 1958). Again, these dying seedlings provide a relatively labile source of N, such that over the growing season, N inputs from seedling thinning are 66–170% of N inputs from decomposition of litter senesced at the end of the growing season (V. T. Eviner and C. E. Vaughn, unpublished data).

The large amount of N released from senesced litter and seedling thinning is retained through the high uptake rates of plants and microbes. While NO_3^- uptake by biota is considerable (Jackson et al. 1989; Schimel et al. 1989; Davidson et al. 1990), both the plant and soil microbial communities take up substantially more NH_4^+ than NO_3^- (microbes take up 4–5 times more NH_4^+ than NO_3^-, plants 30–250% more). The soil microbial community can take up N at a much

higher rate than plants (up to 5–11 times more $^{15}NH_4^+$ and 2–3 times more $^{15}NO_3^-$ over 8–24 hours) (Jackson et al. 1989; Davidson et al. 1990). It is important to recognize that these conclusions are drawn from short-term competition experiments (24 hours or less), and that inorganic and microbial N pools can rapidly turn over in these soils. The mean residence time (MRT) in bulk soil has been calculated as 1.6 days for NH_4^+, 8.4 days for NO_3^- (Herman et al. 2003), and 17 days for bacterial biomass N (Herman et al. 2006). Each time the microbial N turns over, a fraction of it is taken up by the plants, so that over time, an increasing proportion of a given N pulse will be seen in plant biomass (Jackson et al. 1989). Total pools of N in plant versus microbial biomass can vary substantially. Different studies have shown that N pools are higher in the microbial biomass than in plant biomass (Jackson et al. 1988), higher in the plant pool (Jones and Woodmansee 1979), or that the relative size of these two pools can change seasonally within a given site (Jackson et al. 1989).

Seasonal Dynamics in California Annual Grasslands

While a static budget can provide a quick glance at the important nitrogen pools and fluxes in California grasslands (Tables 8.1, 8.2), it can be a misleading representation of this system. N pools and fluxes vary strongly across seasons, years and sites. While many factors are responsible for high variability in N dynamics, the strong seasonality in these patterns is one of the most pronounced features of California grasslands, and on a gross scale, these seasonal patterns are similar across sites and years (Vaughn et al. 1986; Center et al. 1989). These grasslands are strongly influenced by a Mediterranean climate, which is marked by precipitation in the fall through the spring, with temperatures being low in the winter and high in the summer (Figure 8.1a). Seasonal patterns of ecosystem processes are strongly controlled by the relationship between temperature and moisture. Because the timing of ideal temperature and moisture conditions can vary greatly across sites and years, we will refer to seasons as defined by the moisture and temperature conditions shown in Figure 8.1a, rather than assigning them to months of the year (but see Box 8.1 for an example of the timing of these environmental conditions at one site).

Climate and Plant Growth

The onset of precipitation marks the beginning of the growing season by stimulating plant germination, and temperature during the rainy season controls plant growth rates (George et al. 1988). Because ideal temperature and moisture conditions are out of phase with one another (Evans et al. 1975; Major 1988; Reever Morghan et al., Chapter 7) (Figure 8.1a), there are only brief periods in the fall and spring when temperature, light, and moisture are favorable to plant growth (Figure 8.1b) (Evans and Young 1989; Chiariello 1989). After a brief peak of rapid plant growth in the fall, temperatures decrease and aboveground growth decreases and stays relatively low through the winter, but belowground growth continues (Savelle 1977; Heady et al. 1991). Both aboveground and belowground plant growth rates increase again as temperatures rise in the early spring, and within a few weeks of this temperature increase, most annual root growth has occurred (Jackson et al. 1988). Aboveground growth rates rapidly increase through spring until the system begins to dry out, and the plants begin to senesce (Figure 8.1b). At some sites with a prevalence of late season annuals (e.g., on serpentine soils), a modest amount of plant growth can continue through most of the summer (Chiariello 1989).

Seasonality of N Pools and Fluxes

The patterns discussed in this section, and illustrated in Figure 8.1, are best guesses at general seasonal N dynamics in California grasslands. Given the high variability in nutrient dynamics, there have been relatively few studies across sites and years (Heady 1991) that can be used to generalize patterns of nutrient dynamics. In addition, while some parts of the growing season (e.g., fall wet up and peak biomass) have been intensively studied, data is relatively sparse at other points in the growing season, so these relationships should be viewed as hypotheses to be tested with further studies.

SUMMER

Because most N cycling within the soil derives from litter and newly dead seedlings, we will start at the end of the season, when litter and seeds are produced. As the hot, dry summers begin (Figure 8.1a), most of the dominant annual plants have senesced, and in these senesced plants, 63–77% of aboveground N is in seeds, while the rest is in litter (V. T. Eviner and C. E. Vaughn in preparation). There is no evidence that plants retranslocate N from their roots during senescence (Nambiar 1987; Gordon and Jackson 2000), so root N contents likely stay stable during seed and litter production. Plant nutrient uptake in most annual-dominated interior grasslands is likely minimal (Figure 8.1c) due to the senescence of a large proportion of the vegetation. However, in grasslands with high proportions of summer annuals which germinate in the spring and grow after others set seed (Bartolome 1989), plant N uptake during the summer can be up to 10 kg N/ha, approximately 8% of plant uptake between October and June (Chiariello 1989).

It is often assumed that microbial activity is minimal during these dry months, but there is ample evidence that integrated over the whole summer, microbial pools and fluxes can play important roles in the annual cycling of N (Figure 8.1c). When Hart et al. (1993) added ^{15}N to soils in early summer, 9–15% of added ^{15}N was taken up by the microbial biomass by the end of summer, and soil microbial N (as determined by a chloroform fumigation method) has been shown to reach its annual peak by the end of the summer (Jackson et al. 1988; S. Parker, personal communication).
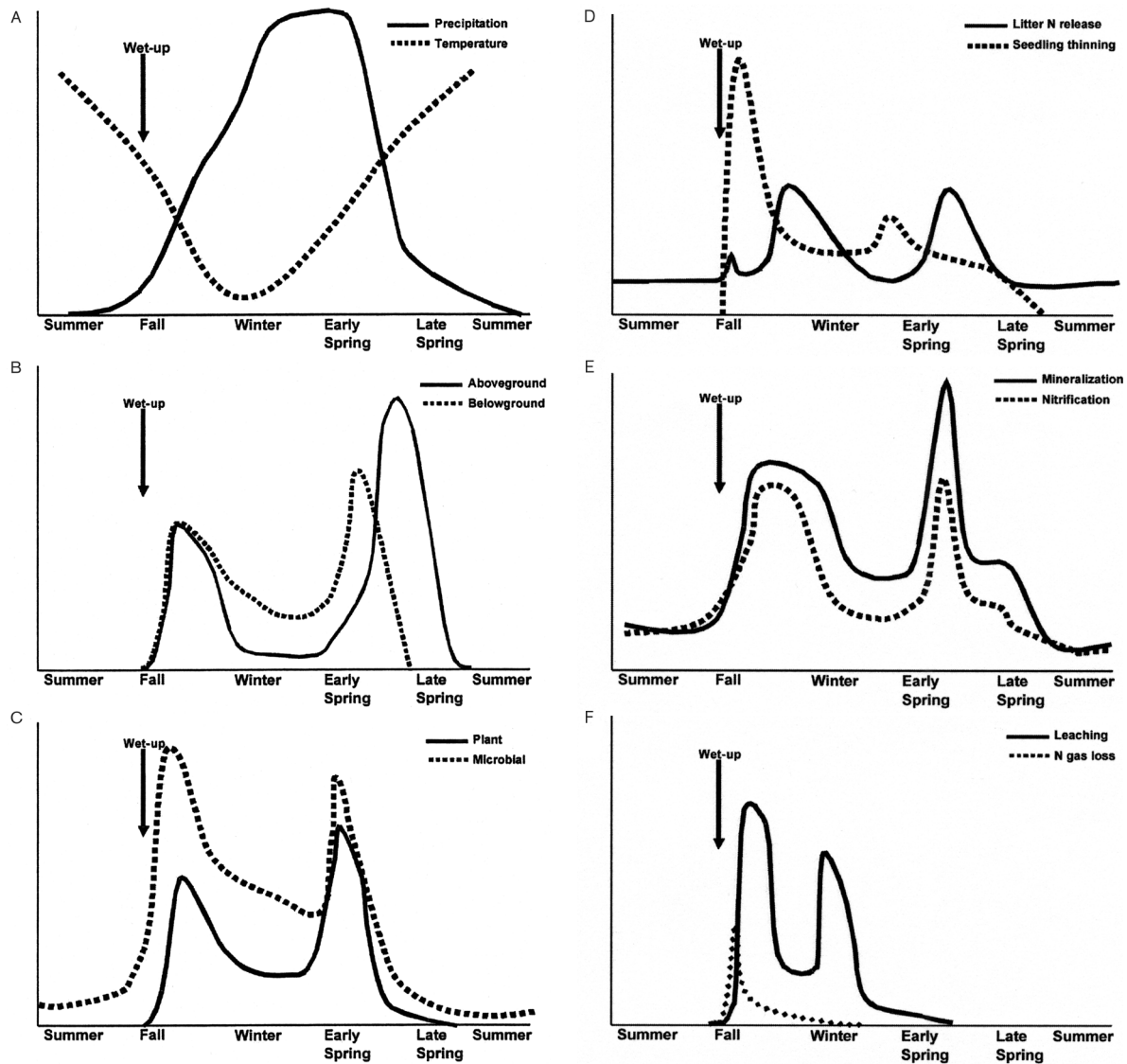
FIGURE 8.1. Seasonal variations in climate, plant and microbial activity, and N dynamics. Other than the temperature and precipitation data (1a), all graphs are approximations of general seasonal patterns based on available studies, many of which do not provide frequent enough sampling dates to determine the exact shape of the graphs. In some cases, studies show different patterns, and these graphs are based on the most prevalent patterns across studies. Graphs are based on (Biswell 1956; Savelle 1977; Jones et al. 1977; Jones and Woodmansee 1979; Woodmansee and Duncan 1980; George et al 1988; Jackson et al. 1988, Jackson et al. 1989; Schimel et al. 1989; Center et al. 1989; Davidson et al. 1990; Heady et al. 1991; Hungate et al 1997; Maron and Jeffries 2001; Cheng and Bledsoe 2002; Herman et al 2003; Corbin and D'Antonio 2004a; Lewis et al. 2006; Eviner and Vaughn unpublished data; J. Corbin and C. D'Antonio, personal communication). (a) Temperature and precipitation (adapted from Evans et al. 1975, and updated with data across California grasslands from the database provided by California Irrigation Management Information System). (b) Plant growth. (c) Plant N uptake and microbial N uptake. (d) N release from litter and seedling thinning. (e) Gross rates of N mineralization and nitrification. (f) N leaching and gas loss.

While litter mass loss is relatively slow over the summer (Savelle 1977), 35% of root litter N and 20% of aboveground litter N is released during the summer (Jackson et al. 1988) (Figure 8.1d). Some litter decomposition may be mediated by photodegradation, which is responsible for litter mass loss in other semiarid to arid regions (Moorhead and Callaghan 1994; Austin and Vivanco 2006). Seed N may be lost or recycled through the system through high granivory rates during the summer affecting 1–75% of seeds (reviewed in Heady et al. 1991).

While net and gross rates of mineralization and nitrification are low throughout the summer (Figure 8.1e), integrated over a whole summer, they can lead to significant accumulations of soil inorganic N, particularly NO_3^- (Jones and Woodmansee 1979; Jackson et al. 1988; Maron and Jeffries 2001; Corbin and D'Antonio 2004a; S. Parker, personal communication). Together, these data indicate that microbes are active at some times or at some locations in the soil profile during the summer, despite low soil water potentials. The frequent presence of morning dew at many grassland sites,

noted in personal observations and personal communications, may episodically stimulate microbial activity at the litter and soil surface during some summer months. Summertime microbial decomposition and N cycling activity are likely to be even higher at sites with substantial fog inputs, which can support late-season plant growth in coastal grasslands (Corbin et al. 2005). Both dew and fog can result in short-term wet-dry cycles, which have been shown to increase microbial activity (reviewed in Fierer et al. 2003b). Because both gaseous and leaching losses of N are highly dependent on water availability, N loss is likely to be minimal during the summer months (Figure 8.1f).

FALL WET-UP

The first significant fall rains (>15 mm) (Figure 8.1a) mark the beginning of the plant growing season (Figure 8.1b) (Heady 1977). Microbial N immobilization is at its peak at wet-up (Figure 8.1c) (Jones and Woodmansee 1979; Schimel et al. 1989; Joffre 1990), with large increases in bacterial and fungal biomass within 24 hours after wet-up, and peaking at

96 hours, coinciding with germination of many plant seeds (Hungate et al. 1997c). At this time, fungal biomass is 3–4 times higher than bacterial biomass (Hungate et al. 1997c).

The rains induce a flush of litter decomposition (Figure 8.1d), with litter leaching accounting for 5% of litter mass loss (Savelle 1977). Rapid germination and death of 50–75% of germinated seedlings (Bartolome 1979; Young et al. 1981) also provide a flush of labile N and C into the system within the first 2–7 weeks of the growing season (Figure 8.1d). These inputs of labile substrates from litter and dying seedlings seedlings may partially account for high rates of N mineralization and nitrification (Figure 8.1e) (Davidson et al. 1990; Maron and Jeffries 2001; Herman et al. 2003). N cycling rates can also be stimulated by wet-up induced lysis of microbial biomass, resulting in substantial short-term (1–4 days) increases in C and N mineralization (reviewed in Fierer et al. 2003b). Increases in soil water potential also stimulate nitrification rates (Stark and Firestone 1995). Despite high initial concentrations and production of inorganic N, N consumption is greater than production (Herman et al. 2003) because of high microbial immobilization.

This high microbial immobilization is not enough to prevent N loss (Figure 8.1f), but N leaching in this system is generally low, even in response to the addition of 100 kg N/ha (Jones et al. 1977). At wet-up, and for a few weeks following wet-up, NO_3^- leaching is at its seasonal peak (Jones et al. 1977; Vaughn et al. 1986; Jackson et al. 1988; Davidson et al. 1990; Maron and Jeffries 2001). At some sites, N leaching is seen every year (e.g., Hopland Experimental Station, Mendocino County), while other sites (e.g., San Joaquin Experimental Range, Madera County) have no measurable N leaching in some years (Jones and Woodmansee 1979; Davidson et al. 1990; Maron and Jeffries 2001). It has been assumed that leaching rates peak shortly after wet-up, then rapidly decrease, becoming negligible within 1–2 months (Jones et al. 1977; Jackson et al. 1988; Davidson et al. 1990), but a 20 year study in the Sierra foothills (Yuba County) consistently detected a second leaching peak in mid to late winter (Lewis et al. 2006). Nitrogen gas losses are often negligible (Jackson et al. 1988), even in response to the application of 100 kg N/ha (Jones et al. 1977). Instantaneous measures of N gas losses are usually low (1–2 ng/cm²/hr) and even when they occasionally reach high levels (13 ng N/cm²/hr), these fluxes are short-lived and have negligible impact on ecosystem N budgets (Hungate et al. 1997c; Rudaz et al. 1991; Herman et al. 2003). NO fluxes increase within 30 minutes after wet up, but decrease after 48 hours, while N_2O fluxes increase for 192 hours after wet up (Hungate et al. 1997c).

FALL/EARLY WINTER

Due to ideal temperature and moisture conditions (Figure 8.1a), early fall is a period of rapid root and shoot growth (Figure 8.1b) and high N uptake by plants (Jones and Woodmansee 1979; Jackson et al. 1988; Center et al. 1989) and microbes (Hart et al. 1993) (Figure 8.1c). Early fall is

also marked by high loss rates of litter mass and litter N (Figure 8.1d) (Savelle 1977; Jackson et al. 1988), particularly from roots (Heady et al. 1991). Steady seedling thinning also provides a continuous source of labile N (Figure 8.1d). Inorganic N levels can be low (Jackson et al. 1988) to moderate (Vaughn et al. 1986) because rates of microbial NH_4^+ consumption are greater or equal to production rates (Herman et al 2003). However, there is a shift from net N immobilization to net mineralization from early fall through winter (Jones and Woodmansee 1979; Schimel et al. 1989; Davidson et al. 1990; Maron and Jeffries 2001; Herman et al. 2003). These changes in microbial activity, along with lower plant N uptake as temperatures decrease, account for rising concentrations of soil inorganic N levels as winter begins (Vaughn et al. 1986; Jackson et al. 1988).

Despite the fact that inorganic N seems to become more available as fall progresses, N leaching losses are low throughout late fall/early winter (Figure 8.1f) (Jones and Woodmansee 1979; Davidson et al. 1991; Maron and Jeffries 2001), and N gas losses are low throughout the remainder of the growing season (Figure 8.1f) (Herman et al. 2003).

WINTER

While aboveground plant growth is generally minimal over the winter, root growth rates vary widely (Figure 8.1b). Root growth may be depressed in the colder months (Center et al. 1989), may continue at a steady slow rate (Savelle 1977; Center et al 1989), or may remain high throughout the winter (Heady et al. 1991). These variations in root growth patterns are most likely influenced by variations in winter temperatures across sites and years but may also be attributed to different patterns of root growth across species and/or difficulties in accurately measuring root growth. Microbial N immobilization (Hart et al. 1993) can also remain high. Winter months are a time of high rates of seedling thinning (Figure 8.1d) (Woodmansee and Duncan 1980), potentially facilitated by frost-related dieback. Aboveground litter mass loss continues through the winter, or even peaks at this time (Center et al. 1989). Total aboveground litter N release is highly variable in the winter. During some years, litter nutrients accumulate due to high rates of N and P immobilization, and in other years, total litter N and P pools decrease, despite increasing concentrations of litter N and P (Woodmansee and Duncan 1980; Hart et al. 1993). The fall through early winter is the period of peak root litter mass loss, with rates greatly decreasing through the winter (Heady et al. 1991). Interestingly, the soil depths at which peak soil decomposition activity occur shift through the growing season. In early winter, decomposition is greatest at a depth of 20 to 30 cm because of higher soil temperatures at this depth. Through the winter, peak decomposition activity shifts from the deeper soil layers toward the soil surface, peaking in the top 10 cm by spring (Heady et al. 1991). Like microbial N immobilization, microbial activity can be high during this season (Jones and Woodmansee 1979), and although little data is available on N

production rates, microbial NH_4^+ production has been reported to roughly equal consumption (Herman et al. 2003).

Nitrogen gas loss is low during the winter (Figure 8.1f) (Herman et al. 2003), even in response to the addition of 100 kg N/ha (Jones et al. 1977). These same fertilizer inputs also resulted in negligible N leaching during the winter (Jones et al. 1977), and whereas most studies have suggested low N leaching during the winter (Jones and Woodmansee 1979; Davidson et al. 1990; Maron and Jeffries 2001), the only comprehensive N leaching study to date (Lewis et al. 2006) has shown that a second peak of leaching occurs late in the winter (mid to late January) (Figure 8.1f) in the Sierra foothills (Yuba County).

EARLY SPRING

Early spring is marked by continued precipitation and a modest increase in temperatures (Figure 8.1a). As temperatures increase, so do rates of plant N accumulation (Jackson et al. 1988) (Figure 8.1c). By the time temperatures begin to increase at a faster rate—approximately 2–4 weeks after temperatures begin to increase (Figure 8.1a)—most root growth (Figure 8.1b) and plant N uptake (Figure 8.1c) have occurred, with 82% of seasonal N uptake completed by this time, even though only 45% of the annual biomass accumulation has occurred (Jackson et al. 1988). This increase in temperature also stimulates a second seasonal peak in microbial activity (Figure 8.1c), which tends to be higher than the first peak in the fall.

Increasing temperatures also enhance the loss of litter mass and N (Figure 8.1d) (Savelle 1977; Jackson et al. 1988), although net accumulation of litter N has also been seen at this time (Hart et al. 1993). Net N mineralization also increases in the spring (Maron and Jeffries 2001; Corbin and D'Antonio 2004a; Cushman et al. 2004) (Figure 8.1e). Low NO_3 availability is evident from the early spring through the end of the growing season (Vaughn et al. 1986; Jackson et al. 1988), suggesting that N consumption rates increase as steeply as N production rates. High microbial N uptake during this period can limit N availability to plants (Schimel et al. 1989; Jackson et al. 1989). N losses are minimal at this time of year (Figure 8.1f), likely due to high biotic N uptake.

SPRING/PEAK PHYSIOLOGY

As temperatures rise (Figure 8.1a), there is rapid accumulation of aboveground plant biomass (Figure 8.1b) (Jackson et al. 1988), so that roots, which made up 60% of plant biomass toward the end of the winter, only constitute approximately 14% of total plant biomass by peak plant biomass (Jackson et al. 1989). There is also a slight increase in microbial biomass N at this time (Jackson et al. 1988), but the plant N pool is greater than the microbial N pool for the only time during the growing season (Figure 8.1c) (Jackson et al. 1989). Root litter mass loss is minimal through late spring (Heady et al. 1991), and aboveground litter mass loss begins to trail off as well (Figure 8.1d) (Center et al. 1989; Eviner 2001). For the first time in the growing season, an accumulation of newly dead seedlings is evident.

Late spring is marked by peak plant biomass, an exhaustion of soil moisture (Reever Morghan et al., Chapter 7), and plant senescence. The duration of plant and microbial activity into late spring largely depends on the availability of soil moisture and therefore on both climatic conditions and soil water-holding capacity. However, regardless of late season precipitation, most annual plants will senesce in the early summer months (Jackson and Roy 1986). At this time of year in the Sierra Foothills Research Station (Yuba County), Jackson and colleagues (1988) found 4.9% of ecosystem N in the microbes, 3.4% in live plant biomass, and 1.3% in dead plant material.

As the system dries out, microbial CO_2 respiration decreases because of moisture limitation (Fierer et al. 2003a; Eviner 2004). Similarly, rates of mineralization (Herman et al 2003; Eviner et al. 2006) and nitrification decrease (Eviner et al. 2006), with nitrification being particularly sensitive to decreases in soil moisture (Davidson et al. 1990; Eviner et al. 2006).

VARIATIONS IN N DYNAMICS IN CALIFORNIA GRASSLANDS ACROSS SITES AND YEARS

Thus far, we have presented the general seasonal patterns of N dynamics in California annual grasslands, but there is substantial variation in the timing and magnitude of these patterns from year to year and site to site (Woodmansee and Duncan 1980; Center et al 1989; Evans and Young 1989). Seasonal patterns of gross mineralization can be better predicted by soil moisture than temperature (Herman et al. 2003), and these mineralization rates largely determine seasonal dynamics of nitrification and N gas fluxes (Herman et al. 2003). However, temperature plays a critical role during the wet season, as wetter, milder winters will enhance not only the magnitude of plant growth, litter decomposition and N turnover, but also their variability (Woodmansee and Duncan 1980; Center et al. 1989).

Fluctuations in temperature and moisture can also alter the rates of biogeochemical cycles. When numerous drying-rewetting cycles occur in the fall, C mineralization will significantly decrease and can remain depressed for up to six weeks (Fierer and Schimel 2002). Changes in weather patterns, particularly in the fall, can also affect plant species composition (Talbot et al. 1939; Pitt and Heady 1978; Reever Morghan et al., Chapter 7), which can impact N cycling (see subsequent discussion). Precipitation patterns are also likely to greatly influence N leaching patterns.

Site differences are also a key factor in determining nutrient dynamics, as extremely different grasslands types are associated with changes in geology and climate across California's landscape. Similar to variations across years within a given site, climate patterns can be directly responsible for changes in nutrient dynamics across sites. Climate differences across sites can also influence the importance of nutrient limitation to plant productivity, as nutrient limitation becomes a stronger determinant of plant production with increased

water availability (reviewed in Harpole et al., Chapter 10). Site differences in soil type and land use history are also strong drivers of biogeochemical patterns (reviewed in Jackson et al., Chapter 9). Soil texture and organic matter content can greatly impact storage, cycling, and movement of water and nutrients and can also alter human land use patterns and community composition of plants, microbes, and soil fauna—all of which contribute to marked site-to-site differences in the patterns and controls over nutrient dynamics (reviewed in Jackson et al., Chapter 9). For example, grasslands on serpentine soils can be markedly different from those on the more prevalent sandstone-derived soils. These serpentine soils have lower nutrient and water availability and can have toxic concentrations of heavy metals, leading to large changes in the biomass and composition of the flora and fauna and to differences in how belowground biota and processes respond to global changes (reviewed in Harrison and Viers, Chapter 12). General seasonal controls over plant and soil dynamics are roughly similar between sandstone and serpentine communities, but serpentine communities often contain later-phenology plant species, which extend the growing season and typical time of nutrient uptake (Chiariello 1989). Not only is nutrient availability lower in serpentine soils, but lower rates of gross N mineralization and higher microbial N immobilization in serpentine versus sandstone soils further reinforce low plant N availability (Hungate et al. 1997). Serpentine soils have also been found to have lower active and total fungal biomass than sandstone soils, possibly due to increased fungivory by nematodes (Hungate et al. 2000c).

Pools and Fluxes of Other Nutrients

There have been far fewer studies investigating pools and fluxes of other nutrients, but we will briefly highlight how some of these are similar to, or different from N dynamics. As with plant available N, plant demand for phosphorus (P), sulfur (S), potassium (K), and calcium (Ca) must partially derive from seedling thinning rather than simply from litter decomposition, suggesting repeated cycling of plant uptake and mineralization throughout the growing season for all of these nutrients (Center et al. 1989). Litter release of P and S are similar to N release (Center et al 1989), and as with N, soil availability of both P and S peaks early in the growing season, then decreases with increased plant uptake (Vaughn et al. 1986). Sulfur shows similar temporal leaching patterns to N (Vaughn et al. 1986), while P has a relatively closed cycle (Woodmansee and Duncan 1980). While plant growth in most temperate ecosystems is limited by N availability, in California grasslands N, P, and S can all be limiting to plant growth, depending on soils and plant species composition (Martin 1958; Jones and Martin 1964; Jones et al. 1970; Menke 1989).

Other nutrients show seasonal patterns that are very different from those of N, P, and S. Potassium release from litter is mainly controlled by early season leaching rather than microbial mineralization, and soil K concentrations show

inconsistent seasonal patterns from year to year (Vaughn et al. 1986; Center et al. 1989). Soil magnesium (Mg) availability also varies with time, without consistent seasonal patterns across years (Vaughn et al. 1986). In contrast to all of the other nutrients discussed, both litter and soil calcium concentrations do not demonstrate large seasonal fluctuations (Vaughn et al. 1986; Center et al. 1989).

Effects of Vegetation Composition on Nutrient Dynamics

It has been well documented that plant species can alter almost every aspect of ecosystems from soil physical structure to hydrology to the activity and distribution of other organisms. Plant-induced changes to any of these ecosystem characteristics can have large effects on nutrient dynamics (reviewed in Eviner and Chapin 2003b). In this section we investigate how vegetation composition influences nutrient dynamics.

SHIFTS IN PLANT SPECIES COMPOSITION IN CALIFORNIA ANNUAL GRASSLANDS

Plant species composition in California annual grasslands can vary greatly across sites (Harrison and Viers, Chapter 12), years (Talbot 1939; Heady 1958; Pitt and Heady 1978), management practices (Jackson and Bartolome, Chapter 17; Reiner, Chapter 18; Huntsinger et al., Chapter 20; DiTomaso et al., Chapter 22), and due to invasions of exotic species (D'Antonio et al., Chapter 6). Such shifts in plant species composition can affect the timing and magnitude of most N pools and fluxes (Jones 1963; Jones et al. 1977; Hungate et al. 1996; Canals et al 2005; Eviner et al. 2006). These differences across species can be so marked that they completely mask the generalized seasonal trends in N dynamics discussed in previous paragraphs (Eviner et al. 2006).

Species effects on N cycling can often be predicted based on a suite of traits, including litter chemistry, exudation rates, and species effects on microclimate (Eviner and Chapin 2003b; Eviner et al. 2006). Litter N content is often presumed to be the main determinant of a plant's effect on N cycling, and thus, shifts in the relative dominance of legumes vs. grasses can have marked impacts on N cycling (Center et al. 1989; Eviner et al. 2006). Changes in N pools and fluxes also occur as a result of shifts in dominant grass species due to their differences in labile C inputs and microclimate effects (Eviner et al. 2006). Although litter chemistry, microclimate effects, and labile C can be used to predict the ecosystem consequences of shifts in vegetation composition, these traits often fail to predict the impacts of forbs on N dynamics because many forbs contain high levels of secondary chemicals, which are low or absent in other grassland species. For example, plant species effects on potential nitrification in the spring can be predicted well by litter C:N ratios for most species (Eviner et al. 2006). However, nitrification rates associated with *Erodium botrys* (filaree) are substantially lower than would be predicted by

litter C:N ratios because of *Erodium*'s high concentration of phenolics, which inhibits nitrifiers (Eviner and Chapin 2005). Similarly, litter decomposition of *Amsinckia douglasiana* (fiddleneck) is very different from what would be predicted based on traits that predict decomposition of other California grassland dominants. *Amsinckia* is a known hepatatoxin of cattle because of its high concentrations of pyrrolizidine alkaloids. These compounds, which inhibit oxidative enzymes in the livers of cattle, similarly inhibit the microbial enzymes that break down litter, thus greatly decreasing decomposition rates of *Amsinckia* litter (Eviner 2001).

In California grasslands, the effects of plant species on N cycling change seasonally because the relative importance of plant traits that control N cycling changes seasonally. For example, species effects on net N mineralization are determined by soil temperature and moisture in the late fall, labile C inputs and live biomass in the winter, and litter C:N ratios and species effects on soil moisture in the spring (Eviner et al. 2006). Many of the relatively new invaders in California grasslands (e.g., *Centaurea solstitialis* [yellow starthistle], *Taeniatherum caput-medusae* [medusahead], *Aegilops triuncialis* [goatgrass]) are active later in the season than the previously dominant exotics, such as *Avena* sp. and *Bromus* sp., and may be responsible for shifts in the season and soil depth at which peak N cycling occurs. Similarly, native summer annuals can greatly extend the phenology of plant N uptake (Chiariello 1989) and likely soil N cycling as well.

The relative effects of plant species on N dynamics change not only seasonally but also with time elapsed since plant establishment. Labile C inputs and species effects on microclimate can alter N dynamics within the first year of a species being at a site, but the impacts of plants change substantially over the years as their "short-term" effects interact with their litter chemistry and effects on soil chemistry and structure. When shifts in vegetation composition occur, the impact of the previous plant community on litter and soil chemistry can persist and influence N dynamics for years after the species have been replaced by other plants (V. T. Eviner, unpublished data). Thus, to understand the effects of vegetation change on nutrient dynamics, it is critical to consider both the former and the current plant community composition.

Shifts in plant species composition not only influence N pools and fluxes but can also greatly affect the importance of N in controlling plant productivity. For example, shifts between grass-dominated and legume-dominated grasslands determine whether N or another nutrient (e.g., P, S) limits plant growth (Jones and Martin 1964; Jones et al. 1970).

COMPARISON OF EXOTIC AND NATIVE-DOMINATED GRASSLANDS

Over the past two centuries, California grasslands have experienced widespread replacement of native species with exotic annual species (Crampton 1974; Bartolome et al. 1986; Schiffman, Chapter 4; D'Antonio et al., Chapter 6). Most comparative studies have focused on differences between

exotic annual grasses and native perennial bunchgrasses, particularly *Nassella pulchra* (purple needlegrass). In general, perennial bunchgrasses allocate more energy to roots than annual grasses (50% in perennials vs. 39% in annuals), and while most root growth occurs in annual grasses by early spring, root growth is more evenly distributed over the growing season in perennials (Heady et al. 1991). While 92–94% of annual roots are within the top 30 cm of soil (50% within the top 5 cm), only 70% of perennial roots are within the top 30 cm, most of these at the 8–30 cm depth (Savelle 1977). The deeper root distribution of perennials increases their access to water late in the growing season, allowing for longer retention of green tissues, longer growing seasons, and greater surface soil water potentials (Brown 1998,; Reever Morghan et al., Chapter 7; Corbin et al., Chapter 13). These differences in root distribution can potentially alter N cycling rates, as well as the depth distribution of N pools and fluxes.

Nitrogen cycling rates may also differ between annual and perennial grasses as a result of differences in the amount and quality of nutrient and carbon inputs. Perennial grasslands lack the high N input through seedling thinning that is common in annual grasslands; while 45% of shoot production turns over during the growing season in annual grasses, only 5% turns over in established perennial systems (Heady et al. 1991). An exception may be in the establishment of perennial stands, when nutrients from thinned seedlings may be an important resource for establishing perennial individuals (V. T. Eviner and C. E. Vaughn, unpublished data).

Perennial grass litter decomposes more slowly than that of annuals (Savelle 1977; Heady et al. 1991), and the quantity of litter N input by perennials is also lower because more N is recycled within the perennial plant, rather than entering the decomposition pathway (Woodmansee and Duncan 1980). Based on all of these factors, we would expect higher rates of N cycling in annual than perennial grasslands. It has also been hypothesized that perennial grasslands should have lower rates of N leaching early in the growing season because of lower N cycling rates and rapid initiation of plant growth and N uptake in response to fall rains (Bartolome 1989). Comparisons between plots planted to annual vs. perennial grasses in California yield contrasting results and, even within individual studies, do not consistently support the hypothesis that annual systems have higher rates of both N cycling and N leaching (Table 8.3).

As expected based on first principles, some studies have seen lower N leaching in perennial vs. annual grass stands (Maron and Jeffries 2001). Corbin and D'Antonio (personal communication), studying experimental plots in a Marin County coastal prairie, found lower N leaching in perennial stands despite equal or higher rates of net N cycling, lower ^{15}N immobilization, and lower plant N uptake by the perennials. Other studies confirm that ^{15}N immobilization is extremely low in stands of perennial grasses (Hooper and Vitousek 1998), and that net N cycling rates are higher in

perennial than annual-dominated plots. In contrast, S. Parker (personal communication), studying experimental plots at Sedgwick Reserve (Santa Barbara County), found that leaching was higher in perennial than annual grass stands, despite the fact that N cycling rates, soil inorganic N concentrations, and N gas losses were lower in perennial systems. Other studies confirm low inorganic N levels associated with perennial plots (Welker et al. 1991; Seabloom et al 2003b), and lower gross rates of nitrification in perennial stands (Hawkes et al. 2005).

The one consistent result across these studies is that the effects of plant species on N leaching are opposite of their effects on N cycling and inorganic N pools (Table 8.3). There are a number of potential explanations for these patterns:

- Annual and perennial stands may have peak plant and microbial activity at different soil depths, so that sampling N dynamics in the upper 10 cm of soil cannot account for leaching patterns.

- Hydrology may account for inconsistencies in N cycling vs. leaching rates. In well-drained soils, available nutrients may be expected to quickly appear in leachate. However, poorly drained soils can allow for a significant lag between soil N production, uptake, and leaching, decoupling these processes over time (S. Parker, personal communication). Annuals and perennials may also greatly differ in their effects on hydrology.

- While N leaching inversely correlates with microbial biomass N (Table 8.3), microbial N immobilization, on its own, cannot account for the disjunct between patterns of N cycling and N leaching, since a higher microbial biomass does not seem to decrease soil inorganic N concentrations in the summer and fall (Table 8.3), the time at which N produced would be vulnerable to leaching during the early season rains.

Differences in patterns across studies (Table 8.3) may be due to site-related factors, such as soil nutrient capital, soil texture, hydrology, climate, or the species identity of the annual and perennial plants. Different annual grass species can differ in their effects on N dynamics (Eviner et al. 2006), so there is no reason to expect that all annual or all perennial grasses should have similar effects on ecosystem dynamics. Clearly, in order to resolve these conflicting results within and across studies (Table 8.3), we need to rethink our assumptions about N dynamics in these systems and carefully design our experiments to encompass multiple soil depths and hydrology. In addition, we may gain important insights into controls over N dynamics by measuring both net (= production − consumption) and gross (= production) rates of N cycling. In the same set of plots in the same season (although during different years), gross rates of nitrification and microbial biomass N were higher in annual than in perennial plots (Hawkes et al. 2005), while net rates were lower in annual

TABLE 8.3

Comparison of N Fluxes and Pools in Perennial (P) vs. Annual (A) Plots

		Corbin and D'Antonio pers. comm. (net rates)	S. Parker pers. comm. (net rates)	Hawkes et al. 2005 (gross rates)	Eviner and Hawkes pers. comm. (net rates)	Hooper and Vitousek 1998	Welker et al. 1991	Seabloom et al. 2003b
N mineralization	Summer	P=A	P=A					
	Fall	P=A	P<A					
	Winter	P>A	P<A					
	Spring	P>A	P<A		P>A			
Nitrification	Summer	P=A	P=A					
	Fall	P=A	P=A					
	Winter	P>A	P=A					
	Spring	P>A	P<A	P=A	P>A			
Inorganic N	Summer	P=A	P<A	P<<A	P>A			P<A
	Fall	P=A	P<A					
	Winter	P>A	P=A					
	Spring	P>A	P<A				P<A	P<A
Fall leaching		P<<A	P>>A					
Microbial biomass N		P>A	P<A	P<A		Low microbial ¹⁵N in P		
Fall plant N uptake		P<A						
Exotic annual grasses studied		Avena barbata, Bromus diandrus, Vulpia myuros	Bromus hordeaceus, Bromus madritensis, Hordeum murinum	Avena barbata, Bromus hordeaceus	Avena barbata, Bromus hordeaceus	—	Bromus hordeaceus	Bromus hordeaceus, Bromus diandrus
Native perennial grasses studied		Agrostis oregonensis, Festuca rubra, Nassella pulchra	Bromus caritinatus, Elymus glaucus, Nassella pulchra	Nassella pulchra	Nassella pulchra	Nassella pulchra, Sitanion jubatum	Nassella pulchra	Bromus caritinatus, Elymus glaucus, Nassella cernua, Nassella pulchra, Poa secunda
Location of experiment (county)		Marin	Santa Barbara	Mendocino	Mendocino	Santa Clara	Sonoma	Santa Barbara

than in perennial plots (V. Eviner, personal communication), suggesting that annual grasses may increase microbial N consumption to a greater degree than they increase mineral N production.

It is also critical to consider seasonal dynamics in annual vs. perennial grasslands. Seasonal patterns of litter mass loss are similar for annual and perennial stands, but differences between annual and perennial stands in the timing and depth of root activity, in soil moisture dynamics, and in seedling turnover (Savelle 1977; Heady et al. 1991) suggest that seasonal N dynamics should differ across these two grassland types. Corbin and D'Antonio (personal communication) and S. Parker (personal communication) found differences in net cycling rates between annuals and perennials in some, but not all seasons (Table 8.3).

There have been fewer studies comparing native and exotic annuals, or native and exotic perennials. A comparison of the native annual grass *Vulpia microstachys* (small fescue) with the exotic annual grasses *Avena fatua* (wild oat), *Bromus hordeaceous* (soft chess), and *Lolium multiflorum* (Italian ryegrass) found that the native had lower shoot C:N, higher decomposition rates of root and shoot litter, and 3.5 times higher N release from its litter after five months (Franck et al. 1997), but there were no differences between native and exotic annuals in ^{15}N partitioning in March (Hungate et al. 1996). Others (J. Corbin, C. D'Antonio, personal communication) found that experimental plots containing native vs. exotic perennial grasses had similar rates of net N mineralization, nitrification, and ^{15}N immobilization. Plots dominated by both groups of perennial grasses had lower rates of N leaching, higher aboveground productivity, and higher N cycling rates than plots dominated by exotic annual grasses. Life history appeared to be more important than origin (native vs. non-native) in determining N cycling rates.

N CYCLING IN OAK-GRASSLAND SYSTEMS

Hardwood rangelands cover approximately 10% of California (Griffin 1977; Bartolome 1987; Gong 2004). Substantial differences in nutrient dynamics have been found in grasslands below oak canopies compared to open grasslands. Overall, oak canopies act as "islands of fertility" compared to open grasslands, increasing soil N and C (Jackson et al. 1990; Dahlgren et al. 1997; Herman et al. 2003; Waldrop and Firestone 2004); N turnover (Herman et al. 2003); N deposition (Knops et al. 1996); microbial biomass (Herman et al. 2003; Waldrop and Firestone 2004); mineralization, nitrification, and potential nitrification (Davidson et al. 1990; Stark 1991; Herman et al. 2003); total and available P (Dahlgren et al. 1997; Waldrop and Firestone 2004); exchangeable Ca, Mg, and K (Dahlgren et al. 1997); pH (Dahlgren et al. 1997; Herman et al. 2003); and N_2O fluxes, while decreasing NO_x fluxes (Herman et al. 2003) and bulk density (Dahlgren et al. 1997; Herman et al. 2003; Tate et al. 2004). It has been a common practice in rangelands to remove oaks (IHRMP 1998),

resulting in rapid decreases in soil nutrient concentrations (Dahlgren et al. 1997), long-term decreases in soil N and C (Ridolfi et al. 1999), and significant increases in soil erosion (IHRMP 1998). The effects of oaks on soil N disappear within 7–9 years after oak removal (Herman et al. 2003).

Seasonal patterns of aboveground and belowground growth differ substantially for oaks vs. annual grasses, with oak leaf and root production peaking in the spring and summer when annual grass growth is minimal (Cheng and Bledsoe 2002). Soils under oaks have higher water-holding capacity, and wet-up and dry-down more slowly than open grasslands (Herman et al. 2003), although the range of water potentials are similar in open grasslands vs. below oak canopies (Jackson et al. 1990; Stark 1991). Maximum soil temperatures in the summer are also lower under oak canopies than in the open grassland (Stark 1991; Herman et al. 2003).

Soil microbial community composition differs substantially underneath oaks versus in open grasslands (Fierer et al. 2003b; Waldrop and Firestone 2004) and this community change mediates biogeochemical cycling. For example, the decomposition of recalcitrant substrates and soil organic matter are enhanced by substrate additions ("priming effect") in the open grassland, but not in oak soils (Waldrop and Firestone 2004). Bacterial communities from open grasslands also appear to be more adapted to wet-dry cycles than microbial communities associated with oaks (Fierer et al. 2003b).

Effects of Other Organisms on N Dynamics

In addition to plant species, many other organisms have strong influences on the structure and function of California grasslands. A number of studies in California grasslands have shown large variations in microbial community composition across sites or experimental conditions (Steenwerth et al. 2002; Balser and Firestone 2005), and that plant species effects on C and nutrient dynamics are likely mediated by shifts in the microbial community (Jackson et al., Chapter 8; Fierer et al. 2003b; Waldrop and Firestone 2004; Hawkes et al. 2005). Variations in the soil microbial community independent of plant communities can also strongly correlate with rates of mineralization, nitrification, and decomposition (V. T. Eviner et al. in preparation). The composition of the soil microbial community can also determine how biogeochemical cycles respond to environmental conditions, such as drying-rewetting (Fierer et al. 2003b), substrate addition (Waldrop and Firestone 2004), changes in temperature and moisture (Balser and Firestone 2005), N deposition, increased atmospheric CO_2, and changes in precipitation (Horz et al. 2004). Soil microbial communities can also indirectly influence nutrient dynamics through their effects on plant species composition. Most species in California grasslands have symbiotic relationships with arbuscular mycorrhizae (AM) (Hopkins 1987), and different plants can foster different communities of arbuscular mycorrhizae (Hawkes et al. 2006). In

particular, exotic grasses not only have different arbuscular mycorrhizae than native grasses, but they also change the composition of the arbuscular mycorrhizae that infect native grasses (Hawkes et al. 2006). These shifts in AM composition and abundance can have large impacts on the amount, timing, and form of N uptake (Marschner 1996; Tanaka and Yano 2005), plant competitive interactions, plant productivity, and plant diversity (van der Heijden et al. 1998; Callaway et al. 2003; Yoshida and Allen 2004).

California grasslands contain many organisms that regularly disturb the soil (Schiffman, Chapter 15; Cushman Chapter 16), and these would be expected to have strong impacts on nutrient dynamics. Ant mounds occasionally enhance soil N availability but more consistently increase P and K concentrations (Beattie 1989). Gophers can disturb up to 30% of the soil surface each year (Hobbs and Mooney 1985). While gopher mounds are generally associated with higher rates of N cycling (Huntly and Inouye 1988), higher rates of N cycling on California gopher mounds have been found in some studies (Eviner and Chapin 2005), but not others (Canals et al. 2003). Gopher disturbances can also alter plant species composition, which affect N uptake by plants and microbes (Canals et al. 2005). Soil disturbance by feral pigs did not affect net mineralization rates in a northern coastal grassland of California (Cushman et al. 2004), although in other ecosystems they generally enhance N cycling (Singer et al. 1984; Vitousek 1986). Soil disturbances that frequently stimulate nutrient fluxes in other systems may not always stimulate N cycling rates in California grasslands because most soil organic N and root biomass is concentrated in the top 5–10 cm of soil. By mixing the surface soil with deeper soils that have lower pools of N and C (Canals et al. 2003), the stimulation of nutrient dynamics in the upper soil profile may be diluted.

Sheep grazing has not been shown to significantly affect the pools and fluxes of plant, litter, microbial, and total soil N (Center et al. 1989; V. T. Eviner, unpublished data) but can increase availability of most nutrients, except for P (Vaughn et al. 1986). Light to moderate cattle grazing also has been shown to have little effect on total soil N and C, and erosion (Dahlgren et al. 1997; reviewed in Jackson and Bartolome, Chapter 17), but can increase available P (Dahlgren et al. 1997), N cycling rates, and microbial biomass N and C, while decreasing aboveground C and N pools by removing standing litter (Firestone et al. 1995; Herman et al. 2003).

California grasslands have high diversity and abundance of soil invertebrates, and these are likely to play a large role in decomposition and nutrient dynamics (Heady et al. 1991). However, to our knowledge, only the roles of earthworms in litter and nutrient dynamics have been well studied in these grasslands. Both native and exotic earthworms are present in California grasslands and stimulate N and P cycling (Winsome and Hendrix 2000). However, exotic earthworms induce higher rates of nutrient cycling than native earthworms do, whereas native earthworms are active for a longer duration

and foster greater plant diversity and nutrient retention (Winsome and Hendrix 2000; Winsome et al. 2003).

Future Research Directions

Studies in California grasslands have clearly demonstrated that nutrient dynamics are extremely variable across sites and years and are affected by the interaction of many biotic and abiotic factors. In order to advance our understanding of nutrient dynamics in this system, it is critical to go beyond the demonstration of variable patterns and build a generalizable, mechanistic framework to understand and predict this variation. In order to accomplish this, it is critical to further explore the impacts of some of these abiotic and biotic factors and to consider their interactions and relative importance. This is particularly important because recent studies have called into question some long-held assumptions about nutrient dynamics in California grasslands. For example, although N leaching losses have been assumed to briefly peak in the early growing season and then tail off, the only comprehensive, long-term study of N leaching has shown that a second leaching peak occurs in the winter (Lewis et al. 2006). Similarly, it has long been assumed that nitrogen cycling rates, and thus leaching rates, are higher in systems dominated by annual vs. perennial grasses. Recent studies not only have shown that we have been wrong in our assumptions about the relative impacts of annuals vs. perennials, but also have demonstrated that plant effects on N leaching do not necessarily parallel their effects on N cycling (Table 8.3)—clearly indicating holes in our understanding of N leaching dynamics.

There are also critical gaps in our understanding of topics as seemingly well established as seasonal patterns of climate and nutrients. To get beyond rough generalizations of seasonal patterns, there is a need for studies that sample plant and soil nutrient pools and fluxes more frequently (e.g., every two weeks) and explicitly link these to temperature and moisture regimes rather than the time of year. This will be particularly important in understanding and predicting nutrient dynamics and plant growth in response to a changing climate, in which both temperature and precipitation regimes are predicted to change in magnitude and timing (reviewed in Dukes and Shaw, Chapter 19). A tighter link between seasonal and year-to-year variations in climate with nutrient dynamics will also contribute to our understanding of site-to-site variation as climate patterns strongly differ across latitude, longitude, and altitude. But to further advance our understanding of nutrient dynamics across California grassland sites, it is critical to study these climatic variations over time in the context of site differences in soil type, biotic composition, land use history, and current land management to determine their relative importance and interactions.

Both within and across sites, there are many important biotic and abiotic players, and while it has been well established that soil type, plant species, microbial communities, soil fauna, small mammals, livestock, and human activities

can each impact nitrogen dynamics, consideration of any of these factors in isolation can produce misleading conclusions about patterns and controls over nutrient dynamics (e.g., Eviner and Chapin 2005). Furthermore, while nitrogen and carbon have been relatively well studied, there are many other nutrients in California grasslands that can play critical roles in communities and ecosystems (reviewed in Harpole et al., Chapter 10), and, in fact, can be more important than nitrogen in certain sites and seasons (e.g., Ca in serpentine areas, S and P in certain soil types and in legume-dominated sites). The interactions of these biogeochemical cycles can be a critical missing link in our understanding of these communities and ecosystems (Eviner et al. 2000; Eviner and Chapin 2003a). While it is certainly challenging to integrate the individual and interactive effects of so many biotic and abiotic variables, embracing this complexity can move us far beyond discussions of patterns of variability to a mechanistic and predictive understanding of nutrient dynamics and feedbacks, which will be a critical tool for managing and conserving these ecosystems in a rapidly changing world.

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