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Ecological Consequences of Prairie Dog Disturbances

Prairie dogs alter grassland patch structure, nutrient cycling, and feeding-site selection by other herbivores

April D. Whicker and James K. Detling

Disturbance within an ecosystem can change structural and functional properties of that system, creating recognizable, well-defined patches (White and Pickett 1985). The properties that are affected and the extent of their change are directly related to both the natures of the disturbance and of the ecosystem. While it is easy to visualize large areas of landscape significantly modified by physical disturbances such as drought, fire, or hurricanes, it is somewhat more difficult to envision modification by biotic forces, except perhaps by insect outbreaks. In North American grasslands, however, prairie dog (*Cynomys* spp.) colonies provide large and distinct patch structures.

Prairie dogs (Figure 1) are large (approximately 1 kg as adults), herbivorous rodents that burrow and live colonially. Historically, the most abundant and widely distributed species, the black-tailed prairie dog (*Cynomys ludovicianus*), was common throughout the short- and mixed-grass prairies of the Great Plains. It is impossible to estimate accurately the average size or density of prairie dog colonies in presettlement times, but they covered about

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Figure 1. Black-tailed prairie dogs (*Cynomys ludovicianus*) on a soil mound surrounding a burrow entrance at Wind Cave National Park, South Dakota. As long as a burrow is inhabited, prairie dogs maintain the area around the entrance free from vegetation.

40 million ha in 1919 (Nelson 1919, cited in Summers and Linder 1978). This area represents more than 20% of the potential area of natural short- and mixed-grass prairies (Lauenroth 1979). Because prairie dogs have been traditionally viewed as competitors with cattle for rangeland resources, eradication programs have reduced populations to less than two percent of those several decades ago (Summers and Linder 1978). Currently, where their populations are relatively uncontrolled by humans, prairie dog colonies range in size from tens to hundreds of hectares (Dahlsted et al. 1981, Knowles 1986) at average den-

sities of 10 to 55 animals/ha (Archer et al. 1987, Knowles 1986, O'Meilia et al. 1982). However, the size of a single colony may fluctuate dramatically during its decades of habitation, and colonies also may be abandoned or become extinct.

Areas inhabited by prairie dogs receive continual and intense disruption by burrowing and grazing. Colonies are generally located in sites with deep, productive soils where flooding is unlikely and the slopes are gentle (<7%)(Dahlsted et al. 1981). A typical burrow system (Sheets et al. 1971) has two entrances, a depth of 1–3 m, a total length of 15 m, and a diameter

of 10–13 cm.

From these dimensions, we calculate that prairie dogs mix approximately 200–225 kg of soil per burrow system. Much of this subsoil is deposited around the burrow entrances, creating soil mounds 1–2 m in diameter. These burrow entrances may number 50–300/ha (Archer et al. 1987, King 1955, O'Meilia et al. 1982, White and Carlson 1984) and represent small patches within a colony (Figure 2) that have physical and chemical properties that may remain altered for hundreds or thousands of years (Carlson and White 1987).

Although prairie dogs generally denude only the zone surrounding entrances to their burrow systems, their grazing activity affects the entire area of the colony. Prairie dogs forage aboveground throughout the year; they also may clip and fell herbaceous vegetation, nipping it near ground level but not eating it, presumably to facilitate predator detection (King 1955). While it has been established that grazing by domestic animals can change ecosystem processes such as primary production, decomposition, plant succession, and nutrient cycling (Ellison 1960, Floate 1981), documentation of similar large-scale effects by native grazers in relatively natural grasslands is rare.

Despite their obvious influence on the ecological history of North American grasslands, their current status as an agricultural pest, and their natural role as agents of intense vegetation disturbance, prairie dog effects on ecosystem structure and dynamics have been virtually ignored or overlooked by those investigating disturbance and patch dynamics (Pickett and White 1985). Prairie dogs create large, distinct patches within the grassland matrix, and ecosystem processes that occur within the patches may proceed at different rates than those outside the patches. Additionally, process behavior within each patch may not be independent of either other patches or uncolonized grasslands. The import and export of propagules, organisms, and nutrients, for example, may be an important linkage among colonies and between colonies and adjacent grasslands.

Our research has been conducted in the mixed grass prairie at Wind Cave National Park (WCNP), South Da-
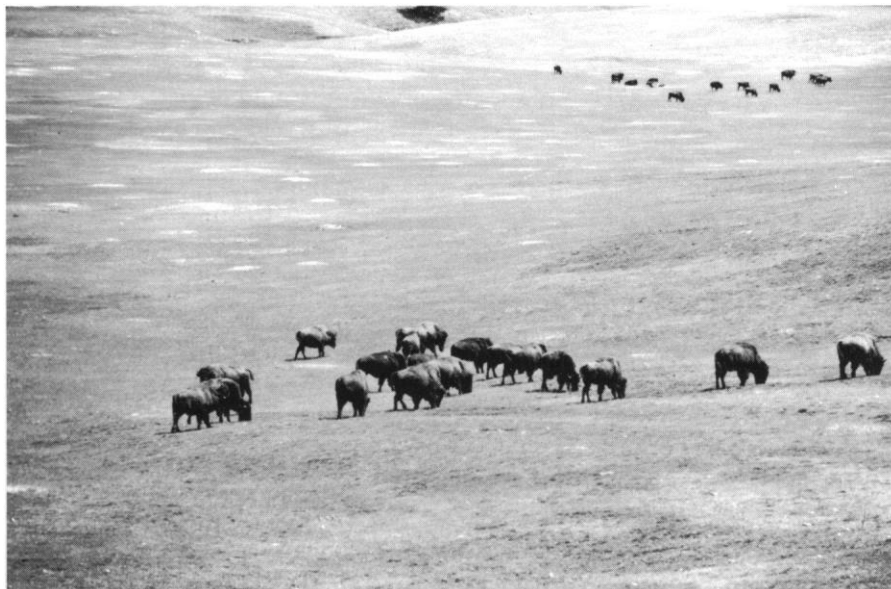
Figure 2. Bison grazing on short-cropped grass on a portion of a large (>100 ha) prairie dog colony. Small, light-colored bare areas are individual soil mounds around prairie dog burrow entrances. Bison spend a disproportionately large amount of their time during the summer months grazing on areas such as this.

kota. This 11,355-hectare site is approximately 75% grassland, and in 1978 it contained 11 major prairie dog colonies (Figure 3) ranging in size from 5 to 250 ha (Dahlsted et al. 1981). Our objectives have been to investigate how black-tailed prairie dogs influence structural and functional properties of the grasslands over time. We are also determining how prairie dogs and other herbivores respond to grazing-induced changes in the ecosystem.

Aboveground patch structure and change

The vegetational structure of a patch can be altered directly and indirectly by prairie dog activity. Prairie dogs repeatedly clip and graze plants, rarely allowing shoots to reach full size. Therefore, canopy height within a colony (5–10 cm) is generally less than half that of nearby, uncolonized grassland (20–30 cm) (Archer et al. 1987, Whicker and Detling in press).

Such direct alteration of vegetation by prairie dog grazing can lead to indirect effects, for example replacement of one ecotype by another (Detling and Painter 1983, Detling et al. 1986). Populations of perennial plants subjected to heavy grazing are typically shorter and more prostrate

than populations that have received little grazing. Such morphological differences can be plastic (i.e., plants return to their original morphological state when released from grazing) or the result of genetic differentiation in the population (Painter 1987). Our work with four dominant grass species at WCNP suggests that genetically distinct ecotypes occur in populations from colonized and uncolonized areas. Both "tall" and "dwarf" morphs exist in the unmodified grassland, but the tall morphs are dominant (Detling et al. 1986). In less than 12 years (Detling and Painter 1983), and possibly much less (Archer et al. 1987, Painter 1987), intensive grazing by prairie dogs shifts the dominance to dwarf morphs that may be more grazing tolerant or, because of their reduced stature, be less intensively grazed than the taller morphs (Jaramillo and Detling in press).

Grazing may also change the competitive balance among species within the colony and modify the microhabitat. These modifications create a mosaic of plant community types within the colony patch. Changes in plant species composition have been observed on many prairie dog colonies (Agnew et al. 1986, Bonham and Lerwick 1976, King 1955, Koford
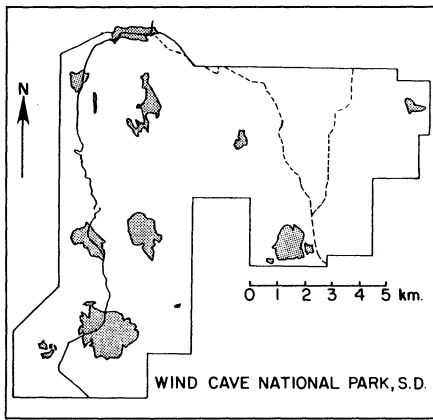
Figure 3. Map of Wind Cave National Park, South Dakota. Solid and dashed lines represent roads, shaded areas represent prairie dog colonies.

1958, Osborn and Allan 1949), but usually not until after two or more years of colonization (Archer et al. 1987, Coppock et al. 1983a). Thereafter, shortgrass species and annual forbs (flowering herbaceous plants exclusive of grasses) become abundant and replace mid-height or tall grasses, and this change also contributes to reduced canopy height. Continual heavy grazing, in conjunction with system specific factors, may eventually result in complete dominance by a few species of forbs or dwarf shrubs.
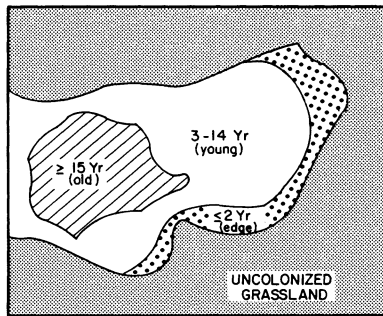
The plant community types on a prairie dog colony are roughly indicative of the extent of herbivore disturbance and reflect the cumulative impact of grazing intensity (i.e., density of animals), grazing duration (generally years), activities of other animals, soil characteristics, and weather. We used a similarity index (Sale 1984) based on relative cover to derive a variable of increasing vegetational dissimilarity (i.e., degree of disturbance or impact) compared with the uncolonized state. Although this variable is continuous (calculated from zero to one), vegetation changes can be somewhat discontinuous (Figure 4b). This approach allows us to compare different states of colonization, colonies, and sample dates, and to view changes of ecosystem processes along an ordered sequence of community similarity, even if it is not always smoothly continuous.

Initially, we classified areas in prairie dog colonies by states of coloniza-

tion (Coppock et al. 1983a), each of which was aged relative to other states within a particular colony (Figure 4a): an older area, a relatively young area, and an edge, which may be an area of colony expansion or a fluctuating border adjacent to uncolonized areas. The uncolonized prairie adjacent to a colony was used as a baseline, control site. However, as convenient as this classification may be in some situations, detailed histories of most colonies are not known, and time of occupation is not the sole determinant of vegetation composition (Figure 4). In this discussion, we present results in reference to both state of colonization and to vegetation similarity.

Changes in vegetation composition due to grazing do not necessarily imply a directional change in plant species diversity (Harper 1969). However, a large body of literature suggests that species diversity is maximized under intermediate disturbance regimes (Collins and Barber

A. PRAIRIE DOG COLONY - TIME SINCE COLONIZATION

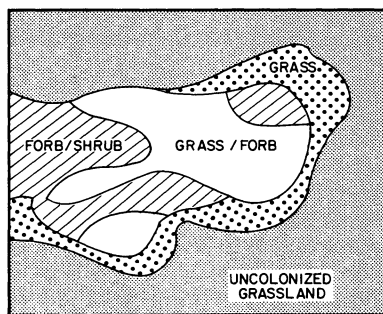B. PRAIRIE DOG COLONY - PLANT COMMUNITY

Figure 4. Schematic of a portion of the same prairie dog colony comparing classification criteria based on chronological age (a) and the similarity of plant community to the uncolonized prairie (b). Changes in the plant community are somewhat indicative of age, but show more variability due to site-specific factors.
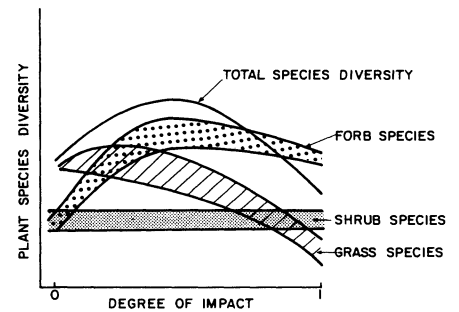

Figure 5. Changes in plant species diversity on prairie dog colonies with increasing impact or disturbance. An undisturbed state is represented at 0 on the x-axis, while a severely disturbed and highly modified system is at 1. Total species diversity is maximized at intermediate disturbances because forb diversity has increased, but grass diversity has not yet substantially decreased. Based on data of Coppock et al. (1983a) and Archer et al. (1987).

1985, Pickett and White 1985). The disturbance imposed by prairie dogs encompasses an entire spectrum of responses by the system (Figure 5), where total plant species diversity is indeed greatest in areas that are occupied an intermediate length of time or that have received moderate impact (Archer et al. 1987, Coppock et al. 1983a).
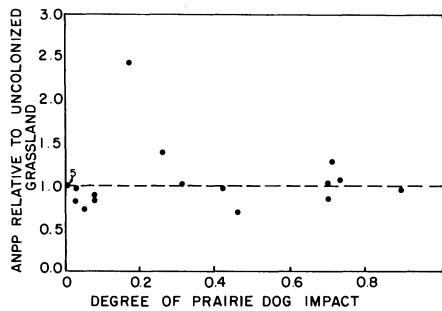
One implication of this diversity gradient is that prairie dogs modify and maintain large areas of the landscape that provide both refugia and propagule sources for plant species (e.g., early successionals) that may only be able to disperse or become established under specific, but spatially and temporally unpredictable, circumstances. Additionally, increased plant species diversity can create habitat and forage diversity that enhances the suitability of an area for other animal species.

## Ecosystem processes and patch dynamics

Grasslands generally support relatively high herbivore loads. Worldwide, native large mammalian herbivores and cattle consume on the average 30–40% of aboveground net primary production (ANPP), while insects such as grasshoppers consume an additional 5–15% of ANPP (Detling 1988). Herbivory may be intense

belowground as well, where invertebrate consumers, principally nematodes, may ingest 6–40% of belowground net primary production in grasslands (Detling 1988).

Rates of consumption on the prairie dog colonies we have been investigating are generally at the upper end of the range reported for native grasslands. Specifically, grass-dominated areas of prairie dog colonies typically lose 60–80% of ANPP to consumption and wastage by prairie dogs and other herbivores. These values contrast with 5–30% consumption rates by herbivores such as bison (*Bison bison*), elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*) on surrounding uncolonized grasslands. Consumption rates on areas dominated by forbs or dwarf shrubs are considerably more variable (10–70% of ANPP), possibly because prairie dogs still inhabit some of these areas but migrate out of similar areas at other sites. As a result of these heavy grazing intensities, aboveground plant biomass on prairie dog colonies is typically maintained at one-third to two-thirds of the aboveground biomass on adjacent uncolonized areas, but the standing live-to-dead biomass ratio is two to four times higher on the colonies (Cop-

Figure 6. Aboveground net primary production (ANPP) of two prairie dog colonies in three different years (1984–1986) in Wind Cave National Park. A disturbance index (prairie dog impact) was calculated as the dissimilarity of colony vegetation to that of uncolonized sites. For highly disturbed areas, the index approaches 1. The number 5 refers to the number of uncolonized sites sampled. The dashed line is the relative ANPP value (1.0) of uncolonized sites. Points occurring above or below the dashed line indicate proportionately different ANPP on colony sites than in the uncolonized grasslands adjacent to those sites. However, data did not differ significantly from 1.0.
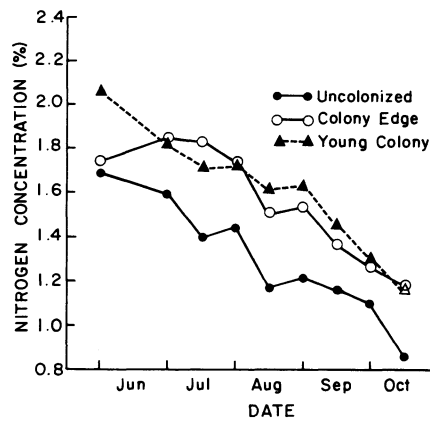
Figure 7. Intraseasonal changes in shoot nitrogen concentration of graminoids collected from a prairie dog colony edge (colonized ≤2 years), a young colony (colonized 3 to 8 years), and an adjacent uncolonized area in 1979. Nitrogen concentration in plants from the young colony and colony edge differed significantly (p<0.001) from that in the uncolonized area. Data are from the study of Coppock et al. (1983a).

pock et al. 1983a, Whicker and Detling in press). Such intensive grazing pressure by these native herbivores affects ecosystem processes such as net primary production and nutrient cycling.

Net primary production. For some East African grasslands, McNaughton (1979, 1986) suggests that net primary production should be maximized at light to moderate intensities of grazing. While such responses to herbivory are commonly observed in aquatic ecosystems (Carpenter and Kitchell 1984, Carpenter et al. 1985), apparently because of rapid nutrient cycling through the herbivores, they have been much less frequently observed in terrestrial ecosystems (Belsky 1986, Detling 1988).

We have collected data on aboveground net primary production from sites representing the four states of colonization from two prairie dog colonies for three growing seasons. Production varied between colonies but increased with increasing spring and summer precipitation. Relative to the adjacent uncolonized grassland, ANPP on the prairie dog colonies did not differ significantly regardless of the degree of impact by the herbivores (Figure 6). However, our results cannot be used to clarify the question

regarding the effects of grazing on production relative to that of purely ungrazed grassland, because the uncolonized grassland used as a baseline for comparison was actually lightly grazed by bison, elk, and other herbivores. Nevertheless, our data suggest that grazing has little or no effect on ANPP in this system over a wide range of grazing intensities, durations of heavy grazing, plant species composition, and weather conditions ranging from drought to above-normal precipitation.

Nutrient cycling. With the exception of much research on fire effects, there has been a notable lack of studies concerning how large-scale natural disturbances affect cycling of mineral nutrients (Vitousek 1985). However, as suggested by their relatively large consumption rates, prairie dogs and other herbivores remove sizable quantities of nutrients (perhaps three-fourths of those translocated aboveground annually) and therefore may substantially influence nutrient cycling. Botkin et al. (1981) hypothesized that cycling of nutrients through herbivores may result in the maintenance of a pool of readily available nutrients near the soil surface. In addition, they suggested that consumption of vegetation by herbivores may stimulate nutrient uptake, resulting in more rapid turnover of numerous elements. Consistent with such predictions, our field studies (Coppock et al. 1983a, Krueger 1986) indicate that grazing by prairie dogs and other herbivores results in a higher nitrogen concentration in the shoots of plants on the prairie dog colonies than in those of the same species in adjacent uncolonized areas (Figure 7).

The higher nitrogen concentration in shoots of more heavily grazed plants probably resulted from some combination of several mechanisms. First, repeated defoliation and subsequent growth of new leaves throughout the growing season likely maintained leaves at a lower average leaf age on prairie dog colonies. Thus, because leaf nitrogen concentration declines with age, the higher nitrogen concentration in these leaves may partly be a function of leaf age structure.

However, the higher nitrogen concentrations may also have resulted

from increased plant nitrogen uptake and translocation to aboveground tissues in the more heavily grazed areas. To address this point, we examined the amount of nitrogen that accumulated in aboveground tissues per unit ANPP on and off prairie dog colonies over three growing seasons (Figure 8). Over the entire range of grazing impacts, nitrogen uptake per unit of ANPP was greater on the prairie dog colonies than in adjacent uncolonized areas. Because ANPP was about the same on and off prairie dog colonies (Figure 6), these results indicate that total nitrogen yield aboveground was greater on the prairie dog colonies than on the uncolonized areas.

These enhanced nitrogen yields may, in turn, result from factors that are either intrinsic or extrinsic to the plant. For example, defoliation-induced increases in nutrient uptake of Serengeti grasses and sedges have been attributed to the greater demand for nutrients of grazed shoots relative to ungrazed shoots (McNaughton and Chapin 1985, Ruess et al. 1983). With defoliation studies conducted in the laboratory, Jaramillo and Detling (in press) found similar results in plants collected on and off prairie dog colonies. Because flow and retranslocation of mineral nutrients from shoots to roots may regulate rates of root uptake (Marschner 1986), Jaramillo and Detling (in press) suggested that declines in retranslocation after defoliation may constitute a signal for increasing the rate of nutrient uptake by plants.

Under field conditions, however, a number of extrinsic factors related to grazing may contribute to increased foliage nitrogen concentrations and aboveground nitrogen yield on prairie dog colonies. For example, these areas may receive greater inputs of nitrogen in available forms (e.g., ammonium and nitrate ions) from excretion products of herbivores that graze preferentially on colonies (Coppock et al. 1983b).

In addition, by reducing plant biomass and cover, and increasing bare soil (Archer et al. 1987), heavy grazing on colonies may cause microclimatic changes in the system. For instance, the soil-water balance may be altered through a variety of potentially offsetting effects (Archer and Detling 1986, Day 1988). A reduc-
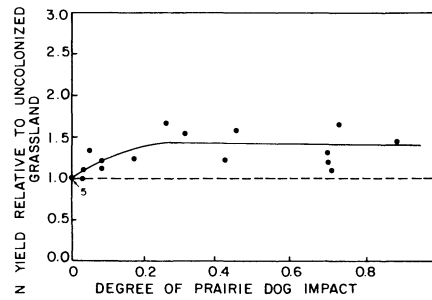
Figure 8. Aboveground nitrogen yield (mg N/g ANPP) on two prairie dog colonies relative to uncolonized grassland. Data are from same colonies and years as those in Figure 6. Horizontal axis is described in the Figure 6 legend. The number 5 refers to the number of uncolonized sites sampled. Points occurring above the dashed line indicate proportionately greater nitrogen yield on colony sites than in the uncolonized grasslands adjacent to those sites. The solid line is fit to the data.

tion in live leaf area and root biomass (Figure 9) may lead to reduced total transpirational water loss from these patches. Similarly, reductions in both live and dead shoot biomass and litter (Archer et al. 1987, Coppock et al. 1983a) could result in a decrease in interception of precipitation by the vegetation (Knapp and Seastedt 1986). Simultaneously, however, increases in bare soil may lead to increases in bare soil evaporative losses. Thus, moisture in the upper few centimeters of soil (the layer from which most bare soil evaporation occurs) may be lower on these heavily grazed sites several days after a rainfall, while soil moisture at deeper depths may be somewhat greater (Archer and Detling 1986).

In addition to potential changes in soil moisture, Archer and Detling (1986) found that soil temperatures averaged approximately 2.5° C higher on prairie dog colonies than in the more densely vegetated uncolonized areas nearby. It is possible that such changes in soil moisture and temperature would lead to increased rates of nitrogen mineralization, at least in the subsurface soil, and hence greater nitrogen availability on prairie dog colonies.

Another mechanism by which heavy grazing might influence nutrient cycling involves competition between soil microorganisms and plants for available nutrients. When the con-

centration of nitrogen in the soil organic matter is relatively low (i.e., the C:N ratio is high), microbes are generally able to outcompete higher plants for the limited supply of available nitrogen. However, as the nitrogen concentration increases, carbon becomes the limiting nutrient and microbes are unable to obtain sufficient organic carbon for growth and metabolism. Holland and Detling (1988) suggest that because grazing by herbivores such as prairie dogs reduces carbon allocation to roots (see below), decomposers become carbon limited in heavily grazed areas. Thus, on prairie dog colonies a larger amount of the nitrogen mineralized is available to plants than in nearby lightly grazed or ungrazed areas.

The extent to which each of the mechanisms described above contributes to grazing-induced increases in plant nitrogen concentration or nitrogen yield is not understood. More research is needed in this area.

The belowground system. Much of the net primary production of grasslands is allocated belowground (Sims and Singh 1978). Soil invertebrates, especially nematodes, are major consumers of root biomass. Because the root system provides a link for transport of materials from the soil to the shoot system, factors that affect the root system generally influence aboveground plant dynamics as well.

Repeated defoliation of shoots reduces belowground biomass at WCNP, where we typically see a marked decline in total root biomass from uncolonized areas to older parts of the colonies (Figure 9). In one study, annual net root production was approximately 40% lower on the colony than in uncolonized grassland, but total nematode densities were 45% higher on the colony than off (Ingham and Detling 1984). As a result of lower root production and higher nematode densities, nematode consumption, as a proportion of net root production, more than doubled. Thus, it appears that the activity of prairie dogs has a substantial impact on both the amount and patterns of energy and material flow occurring belowground. It is also possible that increased herbivory levels on roots of plants on prairie dog colonies represents an additional environmental

stress that limits aboveground primary production as well. The ecosystem consequences of such modifications of belowground functional and structural characteristics are not yet completely understood.

Animal response to patch structure and dynamics

Because prairie dogs create such large, highly modified patches, it is unlikely that other animals remain unaffected by the presence of such patches. Relative to uncolonized grassland, prairie dog colonies often exhibit decreases in arthropod biomass (O'Meilia et al. 1982); increases in both abundance and species number of birds (Agnew et al. 1986); increases in abundance but decreases in species number of other small mammals (Agnew et al. 1986, Hansen and Gold 1977, O'Meilia et al. 1982); and increases in total nematode densities, but decreases in some families (Ingham and Detling 1984). These observations have been implicitly, but not directly, linked to factors such as changes in specific habitat features, interspecific competition, predation, or foraging efficiency.

Ungulate response and grazing facilitation. Coppock et al. (1983b), Krueger (1986), and Wydeven and Dahlgren (1985) quantitatively confirmed earlier anecdotal observations (King 1955, Koford 1958) that bison, elk, and pronghorn preferentially select prairie dog colonies over uncolonized grassland within WCNP (Figure 2). For instance, during five years of study, bison were observed on prairie dog colonies approximately 40% of the time during the growing season, even though colonies comprise only approximately 12% of the observable grasslands in the park.

Bison also differentially use the different states of colonization within each colony. Over the growing season on one extensively studied colony, bison used the younger, grass-dominated portion of the colony for both grazing and resting, the edge primarily for grazing, and the forb/dwarf shrub-dominated older areas principally for resting (Coppock et al. 1983b). The bison avoided adjacent uncolonized prairie. Krueger (1986) found a similar pattern of use within
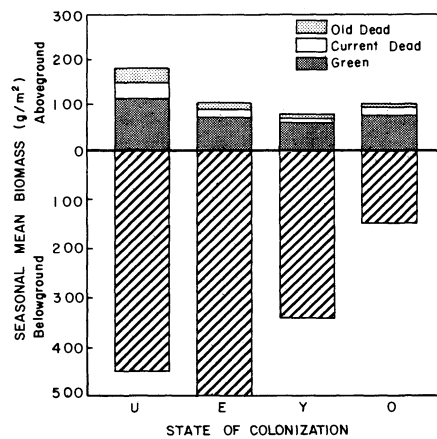

Figure 9. Mean aboveground and belowground plant biomass of uncolonized grassland (U) and the colony edge (E), young colony (Y), and old colony (O) portions of Research Reserve in Wind Cave National Park during the 1984 growing season. "Current dead" refers to plant material that died during the 1984 growing season, while "old dead" material died earlier.

colonies for bison at WCNP, but 57–97% of the pronghorn feeding on colonies were observed on the forb-shrub dominated areas.

Such preferential site selection by bison and pronghorn is not uncommon among ungulates. Large mobile animals can modify activity patterns and site selection over extensive regions that contain a variety of habitat or patch types (Senft et al. 1987). Important criteria for moving between and choosing among feeding sites are the concentration of nutrients in the forage and its accessibility. In patches created by prairie dogs, plant biomass has a greater live-to-dead ratio (albeit lower standing crop), a higher crude protein (nitrogen) concentration, and a greater digestibility than biomass from the uncolonized prairie (Coppock et al. 1983a). These characteristics result in improved nutrition per unit of food consumed on the colony (Coppock et al. 1983b, Krueger 1986), and they may explain feeding site selection for a colony. After the growing season, the nutritional differences between on- and off-colony vegetation are reduced (Coppock et al. 1983a), and bison use of the colonies declines (Coppock et al. 1983b, Krueger 1986).

McNaughton (1976, 1984) has

suggested that on a seasonal basis migratory herds of animals graze patches and improve forage quality for other animals that subsequently feed in those patches, thus facilitating nutrient and energy flow through the ecosystem. The extent to which activities of prairie dogs might improve the nutritional condition of bison has recently been investigated. Vanderhye (1985) used a ruminant nutrition model (Swift 1983) and measured forage parameters from WCNP to simulate potential nutritional benefits (defined as weight gain) accrued to bison by feeding on colonies. Her results suggest that if mature cows randomly use the colonies for feeding, they will gain seven percent additional body weight compared with feeding exclusively outside the colonies. However, typical use of colonies (approximately 40% of time spent feeding) confers an additional 18% weight gain above that from feeding randomly. Yearling bison potentially benefit even more than cows with typical grazing patterns on colonies because of more efficient protein utilization. As sedentary herbivores, prairie dogs appear to facilitate grazing by enhancing forage quality and attracting other animals to the colony.

Just as activities of prairie dogs may facilitate flow of energy and nutrients to ungulates, heavy use of prairie dog colonies by these large herbivores may affect feeding by prairie dogs. In a series of manipulative studies, Krueger (1986) determined that foraging efficiency of prairie dogs was enhanced by the presence of bison on the grass-dominated portions of their colonies. Thus, she concluded that the bison/prairie dog relationship was mutually positive.

Although grazing by prairie dogs may result in nutritional benefits to individuals, its effect on the carrying capacity of the grasslands for herds of large herbivores is not easily determined. Carrying capacity depends on both forage quality and quantity. For instance, we have argued that forage quality is higher on a colony than off; however, the absolute amount of grass (hence, usable nitrogen) available to herds of bison is less on colonies than in the surrounding prairie. This difference occurs because only part of a colony remains grass-domi-

nated (Figure 4), and also because consumption by prairie dogs greatly reduces the standing crop (Figure 9). Thus, the number of animals (e.g., bison) that a region can support will be related in part to this tradeoff of forage quality versus quantity.

Conclusions

From the time they initially colonize new areas, prairie dogs disturb grasslands by their burrowing and grazing, thereby creating large patches of altered vegetation in the landscape. Some features of the altered vegetation, such as reduced canopy height, result largely from the immediate, direct effects of grazing. Others, such as changes in plant species composition or selection for grazing-adapted growth forms, occur slowly and come about through modified competitive relationships among plants after repeated grazing.

This different vegetation structure and composition affects abiotic factors, and these, in turn, contribute to changes in rates of biological processes in the soil. Thus, higher soil temperatures or more favorable moisture conditions in some parts of the soil profile may partially account for increased nematode populations and herbivory, as well as increased activity of decomposer organisms.

Changes in plant physiological and soil processes after grazing may result in enhanced nitrogen uptake by plants on prairie dog colonies. This effect may increase not only the total amount of crude protein available to individual grazers in limited parts of colonies but also the nutritional quality of the forage in those areas. As a consequence, large mobile herbivores such as bison exhibit habitat-use patterns that indicate selection for those areas. We are currently assessing the role of bison in nutrient exchange between colonies and uncolonized grasslands.

We have implicitly traversed a number of temporal and spatial scales in discussing prairie dog disturbance in grasslands. Some processes, such as net primary production, occur during the growing season; others, such as ecotypic differentiation or species replacement, occur over years. Different plant communities can occupy areas of less than a hectare, while bison range over thousands of hectares and may move nutrients or plant propagules from one patch to another. Eventually linking scales of resolution will be critical to understanding how the entire system functions (O'Neill et al. 1986) and responds to disturbance (Pickett and White 1985).

Knowledge of herbivores, disturbance, and ecosystem dynamics is certainly not complete, and a theoretical framework is only currently being built. Therefore, long-term, integrative investigations are necessary to provide a foundation for the expansion of understanding and predictive capabilities.
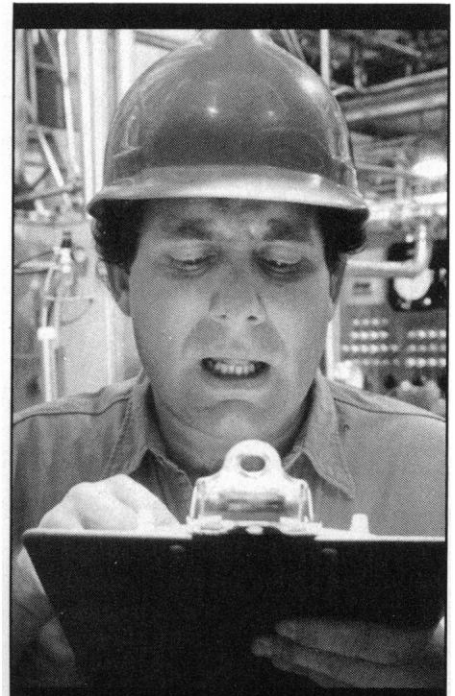
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