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### Population Processes

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Hartnett & Keeler in *The Changing Prairie: North American Grasslands* (Joern & Keeler, editors). Copyright 1995, Oxford University Press. Used by permission.

## Population Processes

David C. Hartnett  
Kathleen H. Keeler

That conditions of life are severe in the [tallgrass] prairie was shown conclusively by the removal of all but one species from a single square meter. ... The remaining sunflowers or goldenrods or grass, profiting from an increased supply of water, light, and nutrients, increased in vigor, size, and production of flowers and seeds.

J. E. Weaver, *North American Prairie*

### POPULATIONS ARE MORE THAN JUST COLLECTIONS OF INDIVIDUALS

Within the prairies, myriad populations of plants, insects, small mammals, and other organisms form distinct levels of organization. The physical forces of weather and fire and the complex networks of species interactions control each species's structure and dynamics and determine its abundance or rarity. Variation in population dynamics and interactions over time and space determine the distribution and abundance of species, and ultimately the composition and dynamics of entire prairie communities.

To the casual observer, plant populations on prairies may seem quite static, like museums containing a diverse collection of specimens that can be seen again and again on repeated visits. Many plant populations, however, are much more analogous to a railway station than a museum, characterized by a constant flux of arrivals and departures. Furthermore, much of the dynamics within prairie plant populations occurs hidden belowground in the pools of seeds and rhizomes, obscuring the true population sizes and their dynamic nature. Even the dominant species that appear to be temporally and spatially stable are not static, but are characterized by significant population flux.

The basic processes determining the sizes and dynamics of all populations are birth, death, and migration. The size of a leadplant population in a tallgrass prairie is determined by the balance between additions of new shoots via both seedling establishment and vegetative reproduction and the death of individuals as a result of competition, herbivory, or physical factors such as drought and fire.

These basic population processes are influenced by a complex set of interacting factors. Fire affects plant populations directly by altering demographic traits and indirectly by influencing plant-herbivore interactions. Water availability, empha-

sized as a major controlling influence in much of early prairie literature (Weaver and Mueller 1942; Weaver and Albertson 1944), has a large influence on plant population dynamics and densities. Populations of many of the prairies' most common species are persistent and highly resilient to environmental stresses such as drought, although their visibility can vary markedly from year to year because of the impact of these stresses on mortality and recruitment. Selective grazing by native ungulates such as bison, soil disturbance by small burrowing rodents, and mutualistic interactions such as those between plants and their pollinators or plants and mycorrhizal fungi all play key roles shaping the structure and dynamics of plant populations, but are not independent of the effects of fire and competition. The interplay of all these factors determines spatial patterns, variation, dynamics, and structure of plant populations across the prairies.

Animal populations respond to a similar set of forces. Population sizes of prairie birds, mammals, insects, and other animals are all affected not only by rates of birth and death, but also by immigration and emigration of individuals resulting from the natural dispersal of offspring as well as habitat changes caused by fire or other factors. An understanding of these processes and the environmental factors that influence them is key to understanding the dynamics of prairies and determining sound approaches to their management and restoration.

The population sizes of many species in the central grasslands, from large mammals such as bison to tiny plants, have been profoundly influenced by human activities since the nineteenth-century arrival of European settlers. The black-footed ferret has declined in number and is now the rarest mammal in North America, primarily because of human efforts to control populations of prairie dogs, the ferret's primary food. Prairie dogs have been reduced to less than 2% of the population size recorded several decades ago (Summers and Linden 1978). *Penstemon haydenii*, the only plant species endemic to Nebraska, is now endangered primarily as a result of human influences on grazing patterns. Even big bluestem, once continuous across the tallgrass prairie region, is now missing from large areas because of plowing, road building, and urbanization.

In this chapter, we provide an overview of patterns in populations of prairie plants, insects, birds, and mammals as well as the processes influencing their numbers. Examples are provided from different types of prairies to illustrate the variation in controlling influences and population patterns across the central grasslands.

#### PRAIRIE PLANTS DISPLAY A VARIETY OF LIFE HISTORIES AND DYNAMICS

Although many different plant growth forms and life history patterns are represented in the central prairies, the dominant species are primarily long-lived perennial herbs. Most prairie plants flower and set seed many times throughout their lives (polycarpic species). After a juvenile period of varying length, during which a plant accumulates a critical threshold level of necessary resources and a critical minimum size, it begins to flower and produce seeds (Roberts et al. 1977; Auffenorde and Wistendahl 1983). Seed production generally increases gradually in successive years with increasing size. A few species flower and produce seed only once in a lifetime (monocarpic species), often after years of vegetative growth. Yet another group, the annuals, complete their life cycle from seed to seed within a single year, but typically have many years of seeds lying dormant in the ground.

Many of the dominant perennials are long-lived (Anderson 1946; Wright and Van Dyne 1976; Gatsuk et al. 1980). The majority of dominant forbs of tallgrass prairie have life spans of 10 to 30 years (Blake 1935; Weaver 1954), whereas some species—such as the orchid *Spiranthes cernua*, the four-o'clock, the bush morning glory, and the Carolina puccoon—may live much longer (Platt 1976; Weller 1985; Keeler 1991; Antlfinger, unpublished data). The population dynamics of short-lived species may be highly responsive to year-to-year environmental variation. The very long-lived species appear to be well adapted and less sensitive to this temporal variation, however, and it is intriguing to think that many individuals we observe today may have experienced extremes such as the droughts of the 1930s and early 1950s as passing intervals of minor impact on their lifetime reproductive success. Longevities of prairie plants are especially difficult to study because, unlike trees, few species produce woody structures that can be aged and many of the plants live a substantial portion of a human life span or longer. A study of switchgrass in Kansas tallgrass prairie showed that the rate of lateral expansion of clones through vegetative reproduction was remarkably constant from year to year. This suggested that the ages of individual clones could be estimated retrospectively by measuring their diameters. Most of the individuals in the local population studied were estimated to be 14 to 20 years old, although a few of the clones that were several meters in diameter may have been several decades old (Hartnett 1991).

The causes of mortality of established prairie plants are numerous and interacting. Individuals face hazards throughout their lifetimes from physical factors, such as desiccation or fire, or they may succumb to the effects of burial by rodents, herbivory from large mammals, or incessant attacks of grasshoppers, beetles, insects, or fungal pathogens. One of the major stresses for established prairie plants is the effects of competitors. Neighboring plants may decrease survivorship or reproductive success by preempting light, water, nutrients, or the services of pollinating insects. The young seedling is typically the most vulnerable stage, and mortality of prairie grasses and forbs is concentrated among the smaller and younger plants in the population. Because they interact, the actual causes of mortality are difficult to discern. For example, defoliation by herbivores may not kill a plant directly, but may do so by weakening its competitive ability (Hartnett 1990; Louda et al. 1990).

#### MOST PLANT POPULATION REGENERATION IS VIA VEGETATIVE REPRODUCTION

The majority of prairie perennials have two modes of reproduction. They produce new individuals via the sexual reproductive process of flowering, pollination, and seed production, and they also reproduce vegetatively, producing clones of new stems via rhizomes, runners, or similar specialized structures. These reiterated vegetatively produced shoots are referred to as ramets in clonal forbs and tillers in grasses. In the prairies, most successful reproduction and population regeneration is via vegetative reproduction, and regeneration from seed typically plays a minor role (Weaver and Mueller 1942; Tripathi and Harper 1973; Glenn-Lewin et al. 1990).

Ramet or tiller recruits differ from seedlings in several important respects. They are, in most cases, genetically identical to their parent plants, in contrast to the genetically variable offspring produced by the sexual reproductive process and outcrossing. There is some debate, however, concerning the genetic consequences of seed versus vegetative reproduction in these perennial herbs, because many

populations regenerating primarily by vegetative reproduction appear to be genetically just as diverse as those regenerating via seed (Ellstrand and Roose 1987). A mixture of clones can contain abundant genetic variation. In addition, mutations within the developing buds along a rhizome system may accumulate to produce genetically variable shoots, as appears to be the case in goldenrods (Schaal 1988).

Shoots arising via vegetative reproduction can also show much greater competitive ability and higher survivorship than those arising from seed. In many clonal perennials, the rhizome or stolon functions like an umbilical cord, enabling the transport of resources from the parent plant to the offspring shoot to ensure its successful establishment until the time when its own root-and-shoot system is sufficient to successfully compete against well-established neighbors (Hartnett 1983). When one considers the strong competition and other hazards facing new plant recruits on the prairie, and the small amount of stored food reserves contained within a seed relative to the vast supply available to a ramet or tiller, it is not surprising that seedling recruitment typically makes a small relative contribution to plant population regeneration.

The patterns of vegetative reproduction in prairie communities also influence spatial patterns in the prairie vegetation mosaic. Those clonal plant populations characterized by the production of numerous short interconnected rhizomes, or runners, form well-defined clones that are easy to identify, such as those of many bunchgrasses. Other species, such as big bluestem, clover, and leadplant, produce few very long wandering rhizomes, and their interconnections may senesce after a few years. These form widely spreading populations of intermingling clones that cannot be clearly delimited. These variations in clonal growth patterns are important because they affect patterns of competition among populations, and competition is a critical process limiting both seed and vegetative reproduction in many clonal grasses and forbs (Hartnett and Bazzaz 1985; Briske and Butler 1989). The tightly compact clones are "territorial" Their dense clump of stems is not easily invaded by competitors, and only the stems growing at the clone edge experience strong competition from neighbors. In the widely spreading rhizomatous species, all stems experience competition from other species as they wander through the habitat. Plant species with long rhizomes are quite mobile over time. They can potentially sample a large area within their habitat and can be very responsive to local environmental patchiness. For many of the rhizomatous prairie grasses, the local light microenvironment they encounter as they sample their habitat may strongly influence the population dynamics of rhizomes and tillers. As sunlight is filtered through a dense prairie canopy, only a small percentage reaches the soil surface. The canopy also changes the spectral composition of light, absorbing primarily red light and reflecting or transmitting longer-wavelength far-red and infrared light. Thus the soil surface under a dense prairie canopy experiences a low ratio of red to far-red light. Rhizomes of clonal grasses and forbs may respond to red/far red light and sense resource availability, competitor density, or changes in canopy density caused by grazing or fire, and adjust vegetative reproduction and shoot population size to local conditions (Deregibus et al. 1985). An understanding of the controls on dynamics of vegetatively reproduced shoot populations is crucial. Total vegetation productivity and community structure is determined primarily by the numbers of ramets and tillers rather than their sizes.

It is difficult to identify "individuals" in prairie populations consisting of wandering and intermingling clones, especially since connections are often underground. Consequently, some aspects of the dynamics of populations of clonal plants in prairie habitats remain somewhat a mystery and are matters of great interest. Does a single, highly competitive clone eventually expand and eliminate the weaker, such that populations gradually progress toward domination by a single clone covering a large area? The high genetic diversity of prairie plants suggests that this is not often the case. If so, what factors prevent eventual domination by one or a few competitively superior individuals?

In clonal prairie plants, population processes occur at two distinct levels. Patterns of birth and death of whole clones may be very different from the patterns of birth and death of shoots making up each clone. If, for example, drought stress caused a 50% mortality rate of vegetative shoots, it makes a great difference whether this represents the death of 50% of the clones or 50% of the shoots within each clone. The former results in significant loss of genetic variation in the population, whereas the latter causes no change in genetic diversity.

#### POPULATION REGENERATION VIA SEED IS UNCOMMON

Although regeneration by seed is infrequent in prairies, it is not usually limited by seed production, which is quite high for most prairie species. Some workers have reported total seed production in tallgrass prairie as high as 20,000 seeds or more per square meter in good years, virtually a solid carpet of seeds. This is an order of magnitude higher than the seed production of nongrassland habitats (Rabinowitz and Rapp 1980; Potvin 1988), although flowering and seed production decline markedly in drought years and the viability of seeds may be quite limited. Seed production is considerably lower in less productive sandhill (2000 to 3000 seeds per square meter), mixed-grass, and shortgrass prairies, and may be low enough to limit recruitment rates in those habitats (Potvin 1988).

Although seed production may be high, regeneration via seed is a tenuous proposition at best. Successful seedling establishment is a rare event (Anderson 1946; Christiansen and Landers 1966; Rapp and Rabinowitz 1985; Glenn-Lewin et al. 1990). The necessary conditions for successful grass or forb germination and seedling survival may occur only infrequently in time or space; hence, there is a very low probability that a given seed will reach an appropriate microsite for germination and encounter the essential favorable conditions immediately following germination. Factors such as rodent, insect, and fungal predation, induced dormancy (seed dormancy can be induced by the low-light environment created by a dense grass canopy), and plant competition are responsible for the fact that only a tiny fraction of a given year's seed crop may successfully produce new plants (Risser et al. 1981; Potvin 1984; Gurevitch 1986; Collins and Wallace 1990).

Frequent recruitment requires appropriate plant biology. For example, sand dropseed seedlings in mixed- and shortgrass prairie emerge throughout the spring and summer and well into the autumn. This may greatly increase their probability of successful establishment. If some early emerging seedlings succumb to unfavorable weather or inadequate soil moisture, other seedlings soon emerge whose timing may coincide with favorable conditions. Seedlings of prairie grasses ordinarily do not survive unless their adventitious roots become sufficiently established in moist soil to supply the necessary water and nutrients to the pho-

tosynthesizing seedling (Ries and Svejcar 1991). At this point, the seedling can be completely autotrophic (growing on its own photosynthate and not reliant on stored food reserves in the seed) and is considered established and so a "recruit." Drought stress is probably the major cause of mortality of young seedlings, although other factors—such as trampling, grazing by cattle, predation by grasshoppers and rodents, disease, and winter killing—also take their toll. The strongly limiting influence of water availability on successful seedling establishment was once emphasized in a humorous way by Kansas range scientist Kling Anderson, who advised, "The critical factor for native grass establishment is to sow seed just prior to a long wet spell."

Next to the requirement for sufficient moisture, successful colonization of the seedlings' roots by mycorrhizal fungi is likely the most important condition necessary for successful seedling establishment. Mycorrhizae are symbiotic associations between a specific group of fungi and plant roots. Mycorrhizal fungi are ubiquitous in prairies, and almost all the dominant plant species form these associations. These fungi germinate from spores in the soil and produce threadlike vegetative structures called hyphae. Mycorrhizal colonization usually occurs when the developing roots of new seedlings or tillers contact hyphae emanating from germinated spores or from plants with established mycorrhizae. The growing hyphae establish contact with a much greater volume of soil than the plant root can alone, and the hyphae absorb mineral nutrients, transporting them into the host plant root and significantly enhancing plant growth. In return for these benefits, the host plant provides a share of its photosynthetic food production as an energy source to the fungus. Thus this is clearly a mutualistic relationship, much like that of a plant and its pollinators, and both parties benefit from the interaction. Mycorrhizae are particularly important in the acquisition of immobile nutrients such as phosphorus because their hyphae extend considerably beyond the local zones of depletion of these nutrients around roots (Hetrick 1989; Koide and Schreiner 1992). Mycorrhizae provide additional benefits for the host plant for which the mechanisms are not well understood, including reduced water stress and increased disease resistance. Mycorrhizal activity must influence competition among seedlings, between seedlings and established adults, and among established adults, and thus can also exert significant influence on mortality and reproduction of established plants. Because of differential plant species dependencies and growth responses to mycorrhizae, any changes in the activity of these fungi caused by fire or other factors can alter interspecific competitive relationships and relative abundances of different plant species (Hetrick et al. 1989).

Mycorrhizal associations may influence plant competition and population dynamics in additional ways. The hyphae of mycorrhizal fungi may form interconnections among the root systems of neighboring plants and provide a direct pathway for transport of nutrients from plant to plant, much like intershoot translocation via rhizomes in clonal plants mentioned earlier (Chiariello et al. 1982; Newman 1988). Interplant mycorrhizal connections add another dimension to the role of mycorrhizae in increasing seedling survivorship and altering the balance of competition among neighboring plants (Newman 1988). In fact, many of the responses we observe in plant populations to factors such as fire, drought, and grazing may be indirect effects, mediated belowground through changes in mycorrhizal fungi, which direct competitive interactions. These numerous interdepen-

dent effects underscore the notion that the prairie is molded by a complex network of population interactions, above- and belowground.

Flower and seed "predation" by beetles, grasshoppers, weevils, and other animals is also an important process influencing reproductive success in prairie plant populations. While the eating of plants is generically called herbivory, an attack on a seed kills an independent (potential) individual, which is logically like the predation of fox on rabbit. Predation at this stage is often intense, may limit population size, and may occasionally destroy 100% of a given year's seed crop (Platt et al. 1974; Willson and Rathke 1974; Keeler 1980). Studies of various prairie forbs have demonstrated that insect predators can successfully limit seed production and/or plant recruitment (e.g., Platt et al. 1974; Kinsman and Platt 1984; Davis et al. 1987; Louda et al. 1990). Herbivory-induced reduction in seed size can significantly reduce the viability of seeds or competitive success of seedlings in many plant species (Weaver and Mueller 1942; Hendrix 1984). The periodic but unpredictable production of large numbers of flowers and seed crops may enable sporadic escape from infestation and may be the key to the regeneration success and long-term persistence of some populations. The Platte thistle of the Nebraska sandhills prairie is an uncommon perennial, despite its great similarities to weedy perennials. Louda et al. (1990) have shown that predispersal flower and seed consumption by insects, postdispersal seed loss to vertebrates, and high mortality resulting from competition with established plants cause severely limited recruitment of the Platte thistle. The insect seed predators cause major losses that are magnified in each succeeding life stage, resulting, like other prairie plants, in a very low probability that a given seed will eventually produce an adult plant.

Many of these factors that limit successful regeneration from seed may also interact in various ways. For example, seedling competition may influence populations directly by reducing survival, or indirectly by amplifying the negative effects of seed predation (Louda et al. 1990).

#### SEED POPULATIONS BELOWGROUND HAVE THEIR OWN DYNAMICS

For many plant populations, the number of individuals present as dormant seeds buried in the soil far exceeds the number present aboveground as established plants. Buried seeds can be seen as forming a community with its own dynamics, which are determined by the balance between arrivals from aboveground seed production and losses caused by germination, predation, fungal decay, and migration resulting from transport by ants or small mammals. To the ecologist studying seed banks, the seeds in the soil and factors regulating their abundance are of primary interest. The aboveground plants are of lesser importance—a seed's way of producing more seeds.

The dominant perennial grasses and forbs of undisturbed prairie generally do not maintain large or persistent soil seed banks (Blake 1935; Lippert and Hopkins 1950; Rabinowitz 1981). In contrast, some of the less-common short-lived and/or weedy species—such as western yarrow, little ragweed, giant ragweed, common evening primrose, mat spurge, and stickseed—are noted for their great seed longevity, some remaining viable in the soil for decades (Rice 1989). These "soil residents" maintain significant seed banks, enabling them to disperse effectively in time. They can sample a number of years in a sit-and-wait game, opportunistically germinating to produce young seedling recruits during the occasional year when

conditions are favorable. For other species, there may be little or no seed bank. However long the seed bank lasts, the life span of all seeds is finite, and the supply of dormant seeds may become exhausted if favorable conditions for establishment do not follow germination at least part of the time (Lippert and Hopkins 1950).

A few studies have specifically examined prairie seed banks. Rabinowitz (1981) reported a mean density of over 6000 seeds per square meter sampled to a depth of 12 centimeters in Missouri tallgrass prairie. Earlier studies by Weaver and Mueller (1942) and Lippert and Hopkins (1950) revealed a range of 300 to 800 seeds per square meter in undisturbed short- and mixed-grass prairie sampled to a depth of 1.3 centimeters. Recalculation of the seed-bank estimates from these studies on a soil volume-equivalent basis revealed that Rabinowitz's study of tallgrass prairie yielded seed densities almost identical to those reported by Weaver and Mueller (1942) for mixed- and shortgrass prairie sampled to the same depth. Overall, in tallgrass prairie habitats there is no close correspondence between the abundance of particular species in the seed bank and their abundances aboveground. Seed banks of shortgrass prairies in eastern Colorado are similarly dominated by early successional annuals and show poor correlation between relative population abundances aboveground and relative abundances of species in the seed bank (Coffin and Lauenroth 1989).

A persistent seed bank represents a "memory" of previous environmental conditions, containing progeny of survivors of many previous seasons of annually varying environments. A seed bank can buffer a plant population against large fluctuations in number and against the risk of local extinction. It may also retard adaptation to changing environmental conditions. Certainly, it can greatly influence the pattern of population recovery after disturbance (Coffin and Lauenroth 1989). More detailed studies of single-species seed-bank dynamics, including rates of additions and rates and causes of losses from viable seed populations, will add greatly to our understanding of the role of buried seed in the population dynamics of prairie plants and their importance in prairie maintenance and restoration.

#### SMALL-SCALE DISTURBANCE PLAYS A CRUCIAL ROLE IN SOME PRAIRIE PLANT POPULATIONS

In addition to the long-lived perennials that dominate most closed, undisturbed prairie communities, several shorter-lived species depend on various small- and large-scale disturbances for successful regeneration and population persistence (Platt 1975; Platt and Weis 1977). Small-scale patchy soil disturbances are created by the excavations and mound deposition by small mammals, such as pocket gophers and prairie dogs, and the diggings of ants; large-scale disturbances are generated by fire or large mammalian grazers, such as the trampling or wallowing activities of bison. Although each of these processes may cause mortality of some plants, for others they provide patches of soil free of intense competition and essential opportunities for colonization (Weaver 1968; Platt 1975; Keeler 1987; Reichman 1987). It is in these patches of disturbed soil that population regeneration via seed may be significant. Numerous species that produce a large number of small, readily dispersed seeds that germinate and grow rapidly are well adapted to colonize these disturbed patches, which are unpredictable in time and space. These species are unable to become established and compete successfully with the dominant grasses and forbs in undisturbed areas; hence, they are constrained in size by the

patterns and frequency of disturbed sites. These species are typically ephemeral, becoming extinct at a local site as it is slowly invaded by seedlings or vegetative recruits of the more competitive perennials, while dispersing and colonizing newly disturbed patches elsewhere. The continual creation of small soil disturbances and the high fluxes of recruitment and death may be critical factors in the persistence of populations of these fugitive species. Natural environmental factors or human influences that reduce or eliminate populations of small prairie mammals or other soil disturbers are likely to have detrimental consequences for some of the rarer plant species that depend on patchy soil disturbances for successful regeneration. For example, a population of stickleaf (*Mentzelia nuda*) in the Nebraska sandhills declined from 397 to 63 individuals over an eight-year period after the cessation of grazing (and the soil disturbances caused by cattle) (Keeler 1987).

Some species are well adapted to refill small openings or disturbances via vegetative reproduction, but require larger, competition-free patches for successful seedling establishment. For example, Canada goldenrod requires open patches of at least 30 centimeters in diameter for successful seedling recruitment (Goldberg and Werner 1983); however, it can rapidly recolonize smaller openings via clonal spread. The majority of seedlings and shoots that colonize disturbed patches fail, for a variety of reasons, to establish successfully. Those that do survive may persist in the disturbance for only a season, long enough to flower and disperse to newly disturbed sites, even though they are perennials that could live a decade or more.

In the shortgrass prairies, two dominant plant species, buffalo grass and blue grama, have very different responses to soil disturbances. Buffalo grass is characterized by extensive tillering and a sod-forming growth habit. It is capable of extensive lateral spread through rapid growth of long (3-4 centimeters) rhizomes, but its rather large, heavy burs, produced among its leaves or at or near the soil surface, greatly limit its seed dispersal. Like many rhizomatous species, it opportunistically colonizes local disturbed patches via vegetative reproduction. It recovers very quickly and can recolonize disturbed sites within a few years (Shantz 1917; Costello 1944). In contrast, blue grama is a slow-tillering bunchgrass with very short rhizomes (less than 1 centimeter), which limit its rate of horizontal spread. Although it is slower to recolonize disturbed sites via vegetative reproduction, it produces small, light, readily dispersed seeds on a culm well above the height of canopy leaves (Riegel 1941); hence, it can more effectively disperse to colonize other disturbed sites elsewhere. Because these two species tend to dominate many shortgrass prairies of the central and southern Great Plains, their population responses to patterns of disturbance may strongly control the overall community structure and vegetation dynamics in those habitats.

Animal-generated disturbances also create and/or modify microhabitats, allowing new species to colonize or changing the competitive relationships among existing plants. By altering microenvironmental conditions, animal disturbances may give a population a competitive advantage that it lacked in undisturbed microsites. Relict bison wallows in the Kansas Flint Hills tallgrass prairie are depressions on flat, upland soils. The compacted soils of these basins create a unique moist microenvironment in the relatively droughty, shallow-soil uplands that allows species of sedges, rushes, and other species more characteristic of lowland prairie to compete successfully. Wallows also provide open microenvironments suitable for invasion by annual colonizers. Soil disturbances may increase the persistence

and size of a variety of populations and tend to increase the overall plant species diversity in these prairie habitats.

#### FIRE AND GRAZING SHAPE PLANT POPULATION STRUCTURE AND DYNAMICS ON A LARGER SCALE

Fire is a natural component of North American grasslands and has played a significant role in the dynamics of prairies throughout their range (see Bragg, Chapter 4 as well as other recent reviews [e.g., Anderson 1982; Axelrod 1985; Pyne 1986; Collins and Wallace 1990]). Here we focus on the influence of fire on plant and animal population dynamics and interactions. An understanding of these effects is important because the long-term effects of fire on the composition and productivity of prairies are mediated through population-level processes such as seed production, tillering dynamics, and survivorship.

The effects of fire on grass populations have been studied extensively. Spring fire in tallgrass prairies generally enhances their survivorship, growth, seed reproduction, vegetative reproduction, and recruitment (Glenn-Lewin et al. 1990); these effects account, in large part, for the stimulation of overall vegetation productivity in response to burning (Kucera and Koelling 1964; Christiansen and Landers 1966; Zimmerman and Kucera 1977; Svejcar 1990). However, considerable variation in fire effects on flowering and seed production occur among grass species and among prairie habitats (Glenn-Lewin et al. 1990). Cool-season grasses, such as Junegrass, generally show decreased flowering and densities following burning. Tillering and other population responses to burning vary greatly between wet and dry years, and year-to-year weather variation typically exerts a stronger influence on population dynamics than does fire.

Responses of forb populations to prairie fire vary considerably, and the mechanisms underlying their responses are not well understood. Frequent spring burning in tallgrass prairie affects forbs such as prairie coneflower, western ironweed, and wild bergamot by reducing the number of stems and flowering and seed production (Knapp 1984; Davis et al. 1987; Hartnett 1991). Tallgrass prairie fires also influence rhizome production, vegetative reproduction, and ramet population dynamics of the clonal forbs (Hartnett 1990). Variation among forb responses to fire is likely related to timing. For the early emerging and flowering species, spring fires may damage buds or kill plants outright (Lovell et al. 1983). Such fires in tallgrass prairie may indirectly affect later species by creating postfire environmental conditions that alter competitive abilities such that the forbs suffer greater competitive suppression by the perennial grasses (Hartnett 1991). The important influence of competition in grassland plant populations is well recognized (Harper 1977; Fowler 1981; Tilman 1988), and it is reasonable to expect that many of the effects of fire, grazing, small-scale animal disturbances, and other processes in many prairie habitats may be mediated through changing plant competitive interactions.

Fire may also indirectly influence prairie plant populations by altering the population sizes of pollinating or herbivorous insects, the abundance of seed predators, or the activities of large grazers (e.g., Knutson and Campbell 1976; Coppock and Detling 1986; Davis et al. 1987). If fire causes a delay in flowering, a plant population may be thrown out of synchrony with its pollinating insects and suffer reduced seed set. Insect populations change in abundance in response to fire as well. In prairies where very frequent fires result in greater abundance of grasses relative

to forbs, grasshopper populations shift concomitantly toward greater abundances of grassfeeding species relative to forb-feeding species (Evans 1984). Gall-forming insects are another important group of insect consumers, and several dozen species of such insects form galls on prairie grasses and forbs. These and other insects are clearly reduced in abundance with frequent fire, and they increase gradually over the years when sites are protected from fire. The underlying cause of this relationship is unknown. The reduction in insect populations may be caused by the direct effects of fire on the insects, reductions in the nutritional quality of the host plant for the insect, or fire-induced reductions in the host-plant population density. Some insect populations (and levels of insect herbivory) may increase after fire (e.g., Davis et al. 1987).

Large grazers influence prairie grass populations through their effects on seed production, seedling establishment, tillering, and survivorship. These effects may vary, depending on the intensity or timing of grazing or other interacting factors such as drought and fire (e.g., Olson and Richards 1988). As discussed earlier, most of the dominant prairie grasses are clonal and thus characterized by two different levels of population structure and dynamics. Grazing can influence their demography at the whole plant level and/or the level of population of individual shoots or tillers. For example, grazing of the bunchgrass little bluestem in a Texas prairie resulted in the fragmentation of clones (clumps), decreasing their mean size but increasing the total density of clumps in the population. Within clones, grazing resulted in a stimulation of tillering, an extension in the season of tiller recruitment, and an overall increase in the number of tillers per unit area (Butler and Briske 1988). These responses varied considerably, depending on the intensity of grazing, and when herbivory was severe, tiller densities, survivorship, and reproduction all decreased (Butler and Briske 1988). Intense grazing may cause reductions in these bunchgrass populations because their basal areas (clone size) and tiller numbers are reduced to small values, and this increases their probability of size-dependent mortality caused by drought or competition. In crested wheatgrass and bluebunch wheatgrass, drought greatly limits the regrowth potential of clones following grazing via tiller production (Busso et al. 1989). Studies of other grasses have also shown decreases in tiller production and/or survivorship in grasses heavily defoliated during one or more growing seasons (Stout et al. 1980, 1981; Hall et al. 1987; Vinton and Hartnett 1992).

Other population responses of prairie grasses to grazing may be highly variable. Longevities of perennial grasses have been observed to be lengthened (Williams 1970; West et al. 1979), shortened (Canfield 1957), or unaffected by herbivory (Wright and Van Dyne 1976). Tiller recruitment and clone size are decreased by grazing in some species, increased in some species, and unaffected in others. In crested wheatgrass, heavy grazing before culm elongation has little effect on tiller population dynamics, but if it occurs after internode elongation, it results in increased overwintering tiller mortality, and reduces both the number and the height of replacement tillers produced following grazing (Olson and Richards 1988).

We emphasize again that these population responses are important because the maintenance of the production and position of perennial grasses and forbs in the prairie community depends much more on the number of individuals in their populations than on the size of individuals. Differential tiller population responses among species in response to grazing or other stress may cause reduc-

tions in some species and increases in others, influencing species composition and relative abundances within the community (Smith 1940; Neiland and Curtis 1956). Similarly, within a grass population, differential tilling and stem population regeneration among clones may influence the genotypic composition and diversity. Indeed, there is evidence that selection imposed by grazing, and differential responses among clones within grass populations can result in genetic differentiation. Western wheatgrass and blue grama plants from populations that have been historically subjected to repeated grazing show different growth forms and responses to competition or grazing compared with plants from populations that have been protected from grazing for a long time. Populations exposed to selection by repeated grazing become genetically differentiated; grazing-tolerant "ecotypes" emerge in the grazed area, while those protected from grazing for many years display low grazing tolerance, but increased competitive ability (Painter et al. 1989; Polley and Detling 1990).

Forb populations' responses to large grazers have not been well studied, but appear to be quite variable. Because cattle and bison show strong preference for grasses, forb populations are not usually directly affected by their grazing but may be strongly, if indirectly, affected by the changes in competitive interactions accompanying the removal of the grasses. They need not benefit: Some forbs in tallgrass prairie showed evidence of competitive release when growing in patches where bison intensively grazed their neighboring grasses, but other species showed decreased performance in grazed patches (Ward et al. 1991). Forb populations are likely to be significantly affected by the other activities of large animals, such as trampling and dung and urine deposition, and by grazing from pronghorn and deer. Some workers have suggested that a major influence of large grazers on prairie plant populations is an increase in seedling survival and establishment resulting from the hoof action of trampling animals and consequent small-scale soil disturbances (what range managers call the "herd effect"). However, studies comparing seedling demography in areas both subjected to and protected from grazing have yielded little evidence supporting the notion that these large animals increase seedling recruitment (e.g., Salihi and Norton 1987).

#### UNDERSTANDING OF PROCESSES INFLUENCING MANY PRAIRIE ANIMAL POPULATIONS IS LIMITED

Tallgrass prairie has been so thoroughly modified or destroyed that we know very little about the natural processes that regulated the number of animals. The mammalian predators (wolves, bears) are gone; the big herbivores (bison, pronghorn) can no longer migrate across whole states. Other animals, such as prairie dogs, coyotes, and rattlesnakes, have been systematically exterminated; their current numbers and distributions are the result of human activities. Smaller animals, ones that people neither persecute nor promote (e.g., shrews, lark sparrows, and lizards), have been reduced to living on islands of native grassland scattered in agricultural, urban, and suburban areas. A few, such as cardinals, opossums, and painted-lady butterflies, have developed behaviors for living in human-created environments. How important abiotic causes of mortality, such as drought and cold, were to population sizes of prairie species, in comparison with biotic causes of death, such as predators, parasites, and disease, is now impossible to determine.

Even in shortgrass prairie, grazing with its attendant fences has greatly complicated understanding the patterns of animal numbers. Shortgrass prairie would seem less impacted by human-induced changes than mid- or tallgrass prairie, and yet the migratory grasshopper *Melanopus spretus*, which formed the hordes of grasshoppers that descended in such devastating numbers on farmers during the nineteenth century, is the only grasshopper and one of very few animal species known to have gone extinct from the Great Plains. It has not been seen since the 1920s and is believed to have been eliminated as a result of land-use changes in the High Plains of Colorado and Wyoming (Costello 1969; Joern and Gaines 1990).

Despite the devastation of the prairies, especially tallgrass prairie, there are few documented extinctions. Partly this is because the region was so vast that animals survived in sparsely populated areas. It may also be that extinction occurred before we knew what was there: Several flea hoppers from prairie marshes in Illinois are known from only a couple of museum specimens collected in the nineteenth century. The marshes are now gone, and the animals have not been found elsewhere (Opler 1981).

That climatic extremes such as drought affected the abundance of prairie animals seems certain. Historical records indicate that bison died by the thousands in sustained droughts (Roe 1951). Severe winters still kill hundreds of pronghorn. Large-scale prairie fires can destroy ground-nesting birds and mammal populations for hundreds of miles (Reichman 1987; Collins and Wallace 1990). The sizes of prairie animal populations are limited by the availability of food, water, and shelter, just like species in other regions. When those basic necessities are insufficient, there is massive death or migration.

While current evidence suggests that the variable prairie environment—fires, droughts, outbreaks of grasshoppers—drove or exacerbated variation in animal population sizes, probably a good year for one species was a bad year for another. Poor plant growth makes for near starvation for grazers; for their predators, it is a good year to catch grazers, other things being equal. Small mammal species have been shown to respond independently to environmental changes. For example, deer mice increase in number after a tallgrass prairie fire, while prairie voles and harvest mice decrease (Kaufman et al. 1990).

The number of birds in an area shifts within and between seasons, but also changes between years in response to burning and climate. Not surprisingly, migratory bird species and resident birds appear to respond to different environmental factors (Risser et al. 1981).

Invertebrate populations are also influenced strongly by climate and fire, sometimes directly, and sometimes indirectly because of changes in the plant community, predators, or competitors. Year-to-year differences in number are the rule. While many species' numbers can be explained by obvious changes in rainfall or temperature, every group includes species that do not respond noticeably to those factors (e.g., Risser et al. 1981; Joern and Pruess 1986).

The variety of responses is simply the prairie version of the principle that each species has a unique set of biotic and abiotic factors that limit its numbers. The species found in a prairie are a mixture of organisms that are the center, south, or east (etc.) part of their range. The animals at the southern edge of their range will flourish in a cold year; those with desert affinities, in a drought. One consequence of this is that no single management plan benefits all species. In Nebraska's san-

dhills prairie, good grass cover favors the prairie vole and box turtles. In bare sandy areas, Ord's kangaroo rat and the earless lizard prosper. Grazing, mowing, or other disturbance favors the latter; an ungrazed sandhills prairie tends to eliminate them.

#### GRASSLANDS PROVIDE SPECIAL CHALLENGES FOR ANIMALS

In contrast to forests, grasslands offer few places to hide. An animal can run (or fly) away from its enemies, but it cannot climb out of reach into a tree or hide behind the tree. One common response of prairie mammals to this challenge has been to live in large social groups; that is, animals stay together for protection. In the broad open plains, while there is no place for prey species to hide, there is also no concealment for the approaching predators. Studies show that members of a group feeding together can watch more efficiently for predators than can solitary animals. When a predator is sighted, some groups, like pronghorns, simply run away. The fastest animal in North America, pronghorns can outdistance any pursuit if they see it in time (Schmidt and Gilbert 1978). Birds take flight. Prairie dogs also vanish when a predator is seen, but they go belowground into their burrows, rather than leave the area.

Prairie dogs are rodents, a species of ground squirrel, but they have one of the most complex social systems of any rodent. Individuals live in permanent social groups called wards, cooperate with other prairie dogs, recognize and show aggression toward neighbors, and show different, more antagonistic behavior toward prairie dogs they have never seen before (Costello 1970; MacDonald and Hyingstrom 1991). They have more than a dozen different calls that are used to communicate across the prairie dog town (Costello 1970; Slobodchikoff et al. 1986, 1991). A bark warns of danger, and a "jump yip" is given when danger has passed. More impressive, the barks that warn of potential danger are distinctive: a different call is made for hawks, snakes, or coyotes (Costello 1970; Slobodchikoff et al. 1986). Recent work (Slobodchikoff et al. 1991) shows that prairie dogs gave different warning barks when they spotted individual humans, so that there was effectively individual recognition of enemies and communication of that information. Such specificity is useful, the authors suggest, because different humans (or other predators) pose different levels of threat. Recent studies have greatly added to our appreciation of the communication abilities of animals generally, but prairie dogs clearly have evolved a very complex system. Thus social-group living provides multiple watchers whose greater alertness and complex communication systems allow effective escape from predators, despite the openness of the country.

For prairie dogs, there are additional benefits to social behavior. The burrows of prairie dogs are an engineering marvel, with listening rooms for hiding close to the surface before venturing out, false tunnels for confusing the snake or ferret that runs in after a prairie dog, and passages below the living areas for safely absorbing flood waters (Costello 1970; MacDonald and Hyingstrom 1991). All this requires substantial excavation and is much easier if several prairie dogs cooperate. Social groups provide each member with a much better burrow.

Bison, too, live in large social groups, but they do not run from predators. Another defense available to animals living in a group is for the largest and strongest to defend the rest. Faced by predators, such as wolves, bison bulls put themselves

between the cows and calves and the wolves (e.g., Roe 1951; Costello 1969). While wolves may be willing to attack a calf, an alert bull is almost always too dangerous to challenge. The social group offers group defense as a form of protection.

Social groups can also benefit from the knowledge of the oldest members of the group, for example, in finding food, water, and shelter. A single animal has only its own experiences to guide it; a herd has older animals that can teach or show young ones where food or water is. In a climate of extremes, such information may be critically important.

Group living by prairie animals provides many interesting behaviors and responses, but from a conservation standpoint it can be quite difficult. Most social animals have behaviors that promote mating between groups rather than within groups. For example, young male bison are expelled from the parental herd to live as a bachelor herd until they can create a herd of their own. This reduces conflicts within the group and the chance of the group developing genetic defects as a result of inbreeding. However, managing organisms that live in groups of 10 or 100 but mate between such groups is much more difficult for the park or preserve manager than managing animals that live in pairs. Keeping a viable population of, say, 16 pairs of white-tailed deer requires many fewer animals, and much less space, than keeping 16 herds of bison.

Population biology concerns the groups of plants or animals within a species that are the reproductive units and whose success or failure causes species expansion or contraction. The environment crucially shapes the types of populations that are found in an area that survive. In grasslands, long-lived clonal plants and social animals are obvious successful patterns, but much more needs to be learned. When and how seed reproduction takes place, the relative importance of seed banks, and how mycorrhizae affect plant dynamics are among the unsolved questions about prairie plants. So little is known of prairie invertebrate population biology that people may find equally fascinating adaptations to prairies when they have time to look.

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