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Prairie vegetation and soil nutrient responses to ungulate carcasses

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Abstract The impact of large ungulate carcasses on grassland dynamics was investigated by monitoring vegetation and soil nutrients in 50-cm circular zones around the center of bison (*Bos bison*), cattle (*B. taurus*), and deer (*Odocoileus virginianus*) carcasses. An ungulate carcass creates an intense localized disturbance that varies with animal size and the season of death. Unlike other natural disturbances, carcasses deposit a concentrated pulse of nutrients into the soil. One year after death, inorganic nitrogen concentrations were significantly higher in the inner 50 cm at both adult and juvenile carcass sites than in surrounding prairie. Areas around a carcass became zones of fertility that favored different components of the vegetation and stimulated biomass production. Species richness and diversity at the center of carcass sites were lowest 1 year after death, but increased significantly in subsequent years. However, warm-season perennial grasses declined near the center of carcass sites and did not recover. Five years after death, ungulate carcass sites remained disturbed patches that harbored vegetation characteristically different in composition and stature from surrounding prairie. By providing a niche for species not normally found in undisturbed prairie, carcasses increased community heterogeneity and may play an important role in adding spatial complexity to grassland ecosytems.

Key words Disturbance · Succession · Carrion · Tallgrass prairie · Soil nutrients

Introduction

Tallgrass prairie is an assemblage of warm-season perennial grasses interspersed with numerous species of subdominant forbs. Vigorous competition by the perennial plants for light, water, and nutrients normally provides little opportunity for seedling establishment (Abrams 1988; Gibson 1988). A soil disturbance or gap in the canopy is necessary for pioneer, fugitive, and many annual plant species to become established (Platt 1975; Grubb 1977; Platt and Weis 1977). Common disturbances in tallgrass prairie include badger (*Taxidea taxus*) excavations, gopher (*Geomys bursarius*) mounds, bison (*Bos bison*) wallows, and animal trails (Gibson 1989). By providing a niche for plants that otherwise are rarely found in the prairie, these small-scale disturbances increase species richness and spatial heterogeneity (Collins and Glenn 1988).

Dung and urine depositions by large ungulates also can produce gaps in the vegetation and create an exploitable resource for competitively suppressed species. These patches are often ecologically different from the surrounding area (Norman and Green 1958; Steinauer and Collins 1995; Williams and Haynes 1995). Nutrient recycling through ungulate urine can be important in tallgrass prairie, because nitrogen (N) availability frequently limits plant productivity (Seastedt et al. 1991; Blair 1997). High levels of N, however, can shift species composition by selectively favoring forbs and cool-season grasses (Seastedt et al. 1991; Gibson et al. 1993). Thus, N pulses can alter competitive interactions and reduce plant diversity indices (Tilman 1987).

Cattle (*B. taurus*) are the predominant large herbivores on Kansas rangelands, although bison graze on many government and conservation preserves. Predation on these ungulates is virtually nonexistent; however, they routinely die of injuries, old age, lightning, and other natural causes. A 2–3% annual death loss is normal for most cattle herds. Legal, health, and management policies usually dictate removing dead individuals, but carcasses in remote or inaccessible areas commonly remain in situ without disposal. Carrion that is not consumed quickly by vertebrate scavengers is subject to microbial and invertebrate decomposition. During the decomposition of small vertebrate carcasses, underlying soil is infused with nutrients (Bornemissza 1957; Putman

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1978). Although carrion may be a mechanism for nutrient recycling, nutrient pulses from small carcasses are likely qualitatively and quantitatively different than those from large herbivore carcasses.

A decomposing ungulate carcass represents a natural disturbance and a potentially significant source of localized nutrient enrichment in prairie ecosystems which could dramatically alter normal edaphic and floristic characteristics. Despite their ubiquitousness, the effects of large carcasses on grassland vegetation dynamics have not been investigated. Thus, the objective of this study was to assess soil and vegetation responses to ungulate carcasses. Specific questions addressed were: (1) Do ungulate carcasses have a detectable impact on soil nutrients? (2) Are the composition and biomass of vegetation surrounding ungulate carcasses measurably different from undisturbed prairie? (3) What time span is required before the vegetation around an ungulate carcass reverts to predisturbance conditions?

Materials and methods

Study site

Konza Prairie Research Natural Area is a 3487-ha tallgrass prairie in the Flint Hills of northeastern Kansas, approximately 10 km south of Manhattan (39°9’N, 96°40’W). This site is one of the largest tracts of tallgrass prairie in the United States specifically dedicated to ecological research. As part of the Long-Term Ecological Research Program, Konza Prairie is parceled into a series of watersheds (catchment basins) burned at different frequencies (1, 2, 4, 10, and 20 years). Topographically, the area is characterized by level uplands, limestone hillsides, and fertile lowlands. The upland soils are shallow, cherty, silty clay loams (Udic Argiustolls and Lithic Haplustolls), whereas the lowland soils are deep colluvial and alluvial deposits (Pachic Argiustolls). Stream channels and ravines banded by gallery forests meander through the lowlands.

The climate is temperate midcontinental characterized by hot summers, cold winters, and moderately strong surface winds. Average annual precipitation is 835 mm, with 75% of this occurring in the April to September growing season. Mean annual temperature is 13°C, with average minimum and maximum temperatures ranging from –3°C in January to 27°C in July. The average frost-free season lasts 180 days.

Vegetation is typical of native tallgrass prairie and is dominated by warm-season perennial grasses, primarily *Andropogon gerardii*, *Sorghastrum nutans*, and *A. scoparius*. Numerous forb species are widespread and constitute a significant component of the plant diversity. Botanical nomenclature follows Flora of the Great Plains (Great Plains Flora Association 1986).

Approximately 200 bison graze year-round on a 992-ha internal portion of Konza Prairie. Domestic cattle graze in nearby pastures (510 ha) from May to October at a light stocking intensity, but not all pastures are grazed every year. The remainder of Konza Prairie is not grazed, although white-tailed deer (*Odocoileus virginianus*) are abundant. As part of the minimal management strategy at Konza Prairie, animals that die on site are not removed. Coyotes (*Canis latrans*) and turkey vultures (*Cathartes aura*) are the primary vertebrate scavengers in the area, although the vultures migrate in winter (Zimmerman 1985).

Sampling

Carcasses chronicled during a 5-year period included bison that either died naturally or were killed humanely because of nonrehabilitating injury (n=22), cattle struck by lightning (n=4), and deer that died naturally or were salvaged from vehicular accidents on a nearby highway (n=9). Fresh carcasses found in nongrassland sites (e.g., creeks or woodlands) were transported to adjacent prairie when possible. Carcasses were categorized by size as either adults (body mass >318 kg) or juveniles (ungulates with smaller body mass but excluding neonatal calves and fawns).

After scavengers had removed most of the body tissue, the approximate center of the carcass site was marked permanently with a stake. The area of denuded ground was calculated from an ellipse formula after measuring length and width of the longest axis. Vegetation sampling began in late summer of the first growing season after death. Each site was stratified into four 50-cm-wide zones radiating from the carcass center outward to undisturbed prairie (0–50, 50–100, 100–150, and 150–200 cm). Canopy cover of vascular plants was determined for each zone around the center of a carcass site using a modified Daubenmire scale, with cover categories being: <1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, and >95%.

Plant biomass was estimated by harvesting all vegetation within 20×50 cm quadrats to ground level at the end of the growing season. The quadrats were placed in contiguous 50-cm increments extending from the center stake outward to 2 m in two perpendicular transects. Clipped vegetation was separated into appropriate life-form categories (i.e., annual forb, perennial forb, annual grass, perennial grass, or woody), oven-dried at 60°C; and weighed. Harvested vegetation was returned to the site so that any potential seed sources were not artificially depleted. Because most carcass sites were in grazed areas, biomass production may have been underestimated; however, vegetation was not harvested if herbivory around the site was intense.

Soil nutrient levels surrounding carcasses were determined by collecting core samples in late autumn with a 2.5-cm-diameter probe. Duplicate cores were extracted to a 10-cm depth near the plot center and at 50-cm intervals in opposite directions to 2 m out from the center. Soil samples were analyzed by the Kansas State University Soil Testing Laboratory (Brown 1998). Inorganic N (NH_4 and NO_3) was extracted with 1N KCl and analyzed colorimetrically. Phosphorus (P) was determined using a Bray extractant. Exchangeable potassium (K) was extracted with 1N ammonium acetate. Soil pH was measured potentiometrically in a 1:1 soil:water slurry. To compare N concentrations at carcass sites with results of other studies, inorganic soil N was converted to mass per unit area assuming an average bulk density for Konza Prairie soils of 1 g/cm^3 (Turner et al. 1997).

Data analysis

Canopy cover values for individual plant species were square-root-arcsine transformed using the midpoint of the categories (i.e., 0.5, 3, 15, 37.5, 62.5, 85, and 97.5%). Other response variables were log-transformed before analysis to reduce skewness and improve normality. The data were analyzed using the Statistical Analysis System (SAS Institute 1996) as a repeated measure in time with animal size as the whole-plot and years after death and distance from the center as subplots. The effects of animal size were tested using animal (nested within size) as the error term, whereas time effects were tested with the year×animal (nested within size) mean square, and distance effects were tested with the residual mean square. Species richness (the cumulative number of species found) and Shannon’s diversity index ($H' = -\Sigma\, p_i \ln p_i$) were also calculated. But because the total area in each 50-cm zone surrounding a carcass progressively increased (i.e., 0.8, 2.4, 3.9, and 5.5 m^2), richness and diversity could not be compared among distances. These measures are non-linearly related to plot size, and variation in their values increases as plot size decreases (Kwiatkowska and Symonides 1986). However, interannual changes in richness and diversity within the inner 50-cm zone were analyzed as a split-plot with animal size as the main plot and years after death as the subplot. Treatment means that were associated with a significant F-statistic (P<0.05) were separated by Fisher’s least significant difference.

Results

Disturbance size

Decomposing carcasses characteristically created discrete, ellipsoid-shaped patches devoid of vegetation. The initial size and shape of this disturbance, however, depended upon mass of the animal and the season of death. Adult bison and cattle that died in the spring or summer (*n*=9) created a large barren patch (mean area±SE= 4.0±0.5 m^2). Adults that died in the autumn or winter (*n*=5) produced much smaller denuded patches (0.7± 0.4 m^2). Numerous small gaps in the vegetation surrounding adult carcasses were also produced from bones scattered by scavengers. Juvenile animals dying in the spring or summer (*n*=9) created small barren patches (0.6±0.3 m^2), but juveniles dying in the winter (*n*=12) did not have a discernible impact on the vegetation.

Two years after death, remnant barren patches persisted only at sites where adults died in the spring or summer (*n*=5; mean area=0.9±0.3 m^2). Revegetation at other carcass sites formed a patchy canopy over the previously exposed ground. In subsequent years, wide interstitial gaps in the vegetation remained near the center of most carcass sites.

In general, most of the measured variables had a gradient response from the center of the carcass site outward. Soil nutrient and vegetation responses to carcasses, however, did not extend in a symmetrical pattern, producing high standard errors.

Soil nutrients

Inorganic N (NH_4-N+NO_3-N), P, and pH were influenced by interactions among animal size, years after death, and distance from the carcass center. Both soil K concentrations and organic matter levels were not different between the center of carcass sites and surrounding soil in any year (data not shown).

Inorganic N levels at both adult and juvenile carcass sites were higher ($P<0.01$) in the inner 50 cm compared to soil at the 2-m distance 1 year after death (Fig. 1a). Two years postmortem, inorganic N concentrations at adult carcass sites were significantly higher ($P<0.05$) than in surrounding soil, but N levels at juvenile sites did not differ among distances. By 3 years after death, lingering traces of the N pulse remained near the center of adult carcass sites, with concentrations 10 times higher than those in surrounding soil, although the differences were not significant ($P>0.10$).

Phosphorus concentrations were higher ($P<0.01$) in the center of both adult and juvenile carcass sites than in the surrounding soil 1 year after death (Fig. 1b). By 3 years postmortem, extractable P concentrations in the inner 50 cm of all carcass sites remained significantly higher ($P<0.05$) than in peripheral soil.

Mean pH was significantly lower ($P<0.01$) in the center of carcass sites (6.32±0.24) than in the surrounding soil (7.34±0.10). One year after death, pH in the center of adult carcass sites averaged 5.68±0.31 compared with 6.52±0.49 in the center of juvenile carcass sites (Fig. 1c). Soil pH at all distance intervals did not change significantly over time. The pH values for juvenile carcass sites at 3 years after death were not measured.

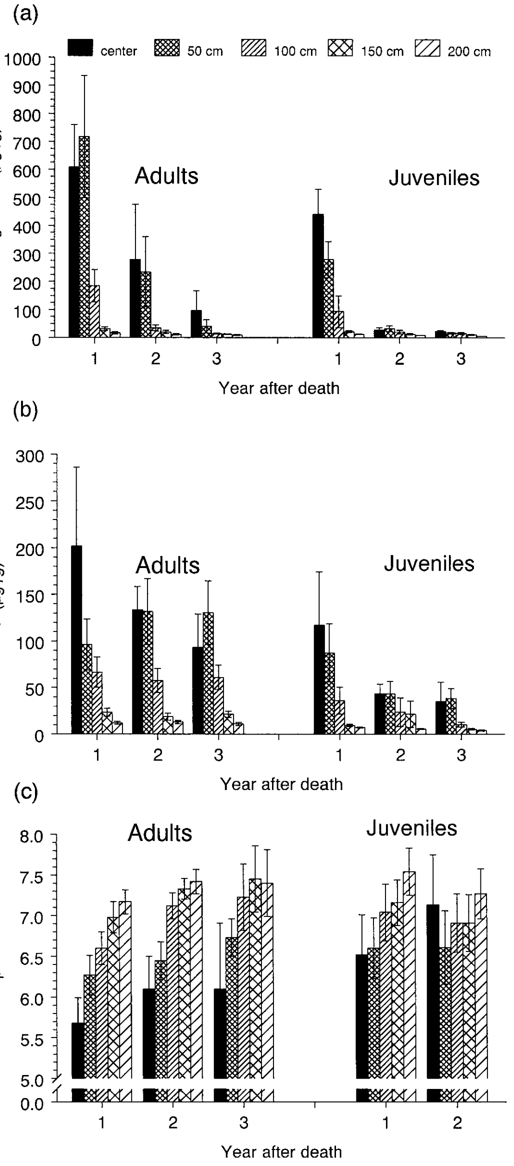

Fig. 1 Average soil concentrations of inorganic nitrogen (**a**), phosphorus (**b**), and pH (**c**) at adult and juvenile carcass sites in 50-cm intervals radiating from the center. Note difference in y-axis scaling. *Vertical bars* indicate SE

Species richness and diversity

Both species richness and species diversity in the inner 50 cm of carcass sites were lowest ($P<0.01$) 1 year after death, but significantly increased in each of the next 2 years before stabilizing (Table 1). In total, across all

Table 1 Mean species diversity (*H'*) and richness (no./0.8 m^{2}) within the 50-cm distance from the center of adult and juvenile carcass sites at successive years after death

Measurement	Adults					Juveniles				
	1 year	2 year	3 year	4 year	5 year	1 year	2 year	3 year	4 year	5 year
Diversity	0.1^{a}	0.6^{b}	0.6^{b}	0.7^{b}	0.5^{b}	0.4^{a}	0.6^{ab}	0.8^{b}	0.7^{ab}	0.9^{b}
Richness	2.2^{a}	5.5^{b}	6.6^{b}	7.0^{b}	6.3^{b}	4.0^{a}	5.6^{ab}	8.1^{b}	8.1^{b}	8.2^{b}

^{a,b} Within each animal size, row means with different superscripts differ ($P<0.05$)

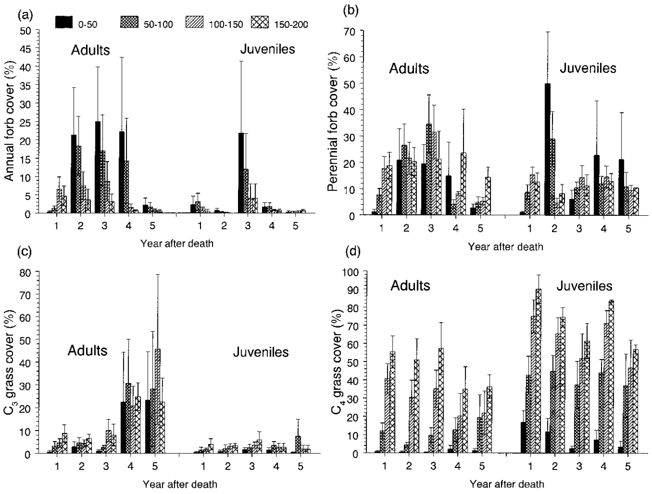

Fig. 2 Average canopy cover (%) of annual forbs (**a**), perennial forbs (**b**), cool-season grasses (**c**), and warm-season grasses (**d**) at adult and juvenile carcass sites in 50-cm zones radiating from the center. Note difference in y-axis scaling. *Vertical bars* indicate SE

5 years of sampling, 55 different species of vascular plants were observed in the inner 50 cm of carcass sites. Annual and perennial forbs composed 62% of the species encountered in the inner zone.

Species cover

Changes in plant species cover at carcass sites varied widely among life forms and individual species within those groups. Canopy cover of annual forbs, perennial forbs, cool-season grasses, and warm-season grasses were all influenced by interactions among animal size, years after death, and distance from the carcass center. Total cover of annual grasses and woody species were not affected ($P>0.15$) by carcasses (data not shown).

Annual forb cover at adult carcass sites was lower ($P<0.005$) in the inner 50-cm zone than in surrounding distances 1 year after death (Fig. 2a). In the following 3 years, however, annual forb cover was significantly higher in the inner zone than in the outermost distance. By 5 years after death, annual forb cover at adult carcass sites was similar among all distance zones. In contrast, annual forb cover at juvenile carcass sites was similar among distances except for a surge in the inner zone at 3 years after death. Successional patterns of the most commonly occurring annual forbs in the inner 50-cm zone indicated sporadic domination by a few species and large interannual fluctuations in cover (Table 2).

Perennial forb cover was lower ($P<0.001$) 1 year after death in the inner 50-cm zone than at other distances at all carcass sites (Fig. 2b). At 2 years postmortem, perennial forb cover was higher near the center of juvenile carcass sites than in the peripheral zone, but did not differ among distances at adult carcass sites. *Ambrosia psilostachya* was primarily responsible for the large interannual fluctuations in perennial forb cover at all carcass sites (Table 2).

Cool-season grass cover increased significantly ($P<0.001$) 4 years after death at adult carcass sites, but

Table 2 Mean canopy cover (%) of commonly occurring forbs and grasses at the 0- to 50-cm distance from the center of adult and juvenile carcass in successive years after death

Species	Adults					Juveniles				
	1 year	2 year	3 year	4 year	5 year	1 year	2 year	3 year	4 year	5 year
Ambrosia artemisiifolia	0	9.0	14.0^{a}	0	0	1.9	0	15.6^{a}	0	0
A. psilostachya	0.4^{a}	20.6	14.0	13.7	2.0	0.1^{a}	49.5^{a}	4.5	21.8	20.3
Chenopodium berlandieri	0	9.4^{a}	0	0	0	0	0	0	0	0
Conyza canadensis	0	0.1	0.6	0	0	0	0	0	0	0
Croton monanthogymus	0	0.1	9.4^{a}	0	0	0.4	0	0.8	1.0	0
Euphorbia glyptosperma	0.3	0	0.4	21.0^{a}	1.2	0	0	0.1	0.2	0.3
Helianthus annuus	0	2.2	0	0.2	0	0	0	0	0	0
Solanum rostratum	0	0.4	0.4	0	0	0	0.6	4.5^{a}	0.2	0
Agropyron smithii	0	0.4	0.4	20.8^{a}	20.8^{a}	0	0	0	0	0
Andropogon gerardii	0.4^{a}	0.4^{a}	0.1^{a}	1.0^{a}	1.0^{a}	4.1^{a}	3.3^{a}	1.6^{a}	6.2^{a}	1.8^{a}
Sorghastrum nutans	0^{a}	0.1^{a}	0^{a}	0^{a}	0^{a}	7.4	7.5	0^{a}	0.2^{a}	1.5

^{a,b} Means within each column with a superscript are different ($P<0.05$) from cover values at the 150- to 200-cm distance from center

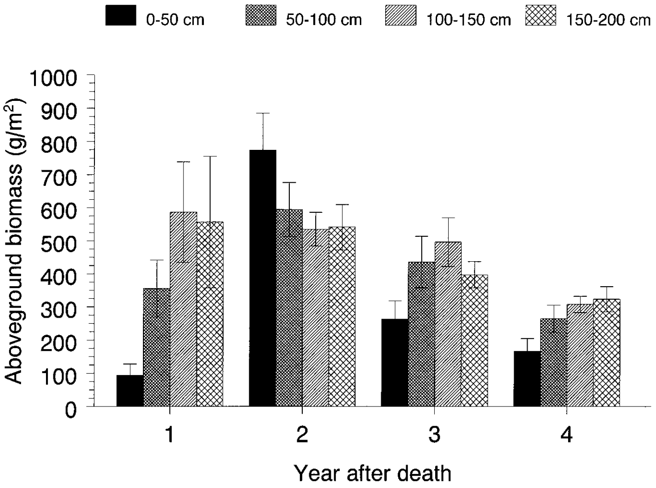

Fig. 3 Average total aboveground biomass at carcass sites in 50-cm zones radiating from the center. *Vertical bars* indicate SE

did not change over time at juvenile carcass sites (Fig. 2c). The cool-season grass cover consisted primarily of *Agropyron smithii*, which proliferated at two adult carcass sites but did not occur at any juvenile carcass site (Table 2). Cover of other C_3 grass species did not change over time at carcass sites. However, cool-season grasses may have been underestimated, because sampling occurred in late summer when these grasses either were senescent or not actively growing.

Warm-season perennial grass cover was lower ($P<0.001$) in the inner 50 cm of all carcass sites than at other distances every year (Fig. 2d). Mean cover of C_4 grasses was lower ($P<0.005$) at adult carcass sites (38.9%±3.0) than at juvenile carcass sites (65.8%±3.7). After 5 years, cover of both *Andropogon gerardii* and *S. nutans* remained significantly lower in the inner 50 cm of adult carcass sites than in the peripheral zone (Table 2).

Biomass

Total aboveground biomass was influenced only by an interaction between year after death and distance from the carcass center. One year after death, biomass was lower ($P<0.001$) in the inner 50 cm than in other distance zones (Fig. 3). By 2 years postmortem, mean biomass in the inner 50 cm increased to 773±111 g/m^2, primarily because of prolific production from *Helianthus annuus* and *Chenopodium berlandieri* at a few carcass sites. In subsequent years, biomass production in the inner 50-cm zone decreased as smaller stature species invaded the sites. Perennial grass biomass was a minor component of the total biomass in the inner 50-cm zone in all sample years. Generally, biomass of the life-form categories mirrored changes in the plant composition patterns (data not shown).

Discussion

Carcasses created unique disturbances, and their effects on prairie vegetation and soil nutrients varied considerably, depending initially upon size of the animal and the time of year it died. When an adult ruminant dies, copious amounts of bodily fluids and decomposition products seep into the surrounding soil. Underlying and adjacent plants are either killed directly by the leachates or smothered under the carcass. A 454-kg ruminant carcass contains approximately 59 kg of digesta (E.G. Towne, unpublished data from 32 ruminally cannulated cattle). This persistent mound degrades slowly and, except for scattered bones, usually constitutes the carcass residuum.

Scavenger activity influences the influx of nutrients from carcasses into the surrounding soil and the subsequent effect on prairie vegetation. Adult carcasses are usually consumed in situ, allowing leachates to concentrate in the soil. In warm weather, decomposition of an adult carcass creates a large denuded patch, because accelerated putrefaction eventually induces vertebrate scavengers to abandon the carrion. In contrast, juvenile carcasses produce small denuded patches because a large proportion of the carcass can be consumed by vertebrate scavengers before spoilage. Additionally, coyotes frequently drag juvenile carcasses from their original locations, dispersing bodily fluids over a wide area. That diluted nutrient flux may have a subtle influence on plant dynamics beyond the immediate sphere of the carcass. In tropical ecosystems, numerous scavengers rapidly dismember carrion and likely reduce potential nutrient recycling from carcasses. However, the carcasses of large herbivores (e.g., elephants, *Loxodonta* sp.) would have a substantial impact on soil and vegetation dynamics regardless of scavenger density (see Coe 1978).

Perturbations created by ungulate carcasses deliver a concentrated pulse of nutrients that exceeds amounts from other natural processes. Although both dung and urine depositions return nutrients to the soil, excretory N is primarily in the urine (Petersen et al. 1956; Betteridge et al. 1986). For cattle, urinary N is distributed in a diffused pattern equivalent to 30–60 g N/m^2 at the center of the patch (Doak 1952; During and McNaught 1961). Because soil N is susceptible to denitrification, leaching, and volatilization losses (Groffman et al. 1993; Williams and Haynes 1994), elevated concentrations in these patches are relatively short-lived. However, residual N concentrations near the center of adult carcass sites averaged 72 g N/m^2 more than 1 year after death, suggesting that initial NH_4-N and NO_3-N levels were extremely high. Thus, ungulate carcasses represent an intense episodic source of nutrient input to the soil.

The flush of nutrients released by an ungulate carcass combined with the killing of vegetation creates a disturbed area where resources are abundant and competition is reduced. Although conditions near the center of adult carcass sites appeared suitable for pioneer species, few annuals had become established in the inner 50-cm zone 1 year after death. Initial NH_4-N concentrations may have been sufficiently high to inhibit plant establishment. Areas surrounding the carcass center, however, became zones of fertility that stimulated biomass production. At one carcass site, aboveground biomass averaged 2655 g/m^2, which is more than 6 times the long-term average for this area (Briggs and Knapp 1995). Annual and perennial forbs composed 63% of this biomass, whereas forb production in tallgrass prairie averages 45 g/m^2 at annually burned sites and 94 g/m^2 at unburned sites (Abrams et al. 1986).

The colonization pattern was not predictable, although a greater variety of annual forbs appeared at adult than at juvenile carcass sites. *Ambrosia artemisiifolia*, *Conzya canadensis*, and *Solanum rostratum* were the most frequently appearing fugitive forbs. Low-growing annuals, such as *Croton monanthogymus* and *Euphorbia glyptosperma*, subsequently became established at sites with bare ground and sparse vegetation. However, most vagrants rarely persisted for more than two growing seasons. A few nonindigenous species associated with disturbed soil, such as *Bromus japonicus*, *Eragrostis cilianensis*, *Setaria glauca*, and *Lactuca serriola*, occurred sporadically but never became abundant. Weedy species commonly associated with local agricultural fields, such as *Abutilon theophrasti* and *Amaranthus retroflexus*, did not appear at any carcass site.

The colonization of annuals depends upon seed availability. Because a carcass does not turn over the soil and expose buried seeds, a different guild of species establish at carcass sites than at other disturbed areas (Platt 1975; Gibson 1989). Many pioneer species at carcass sites likely came from seeds near the soil surface or from seed rain. *Ambrosia artemisiifolia*, *Conzya canadensis*, and *Bromus japonicus* occasionally grow in unburned prairie and could potentially provide a seed source for nearby carcasses. The other early successional species, however, occur only in disturbed soil.

Following the transient surge of annual forbs, revegetation was typically by subdominant species that occurred in the assemblage surrounding individual carcasses. *Ambrosia psilostachya* was the only perennial forb that proliferated near the center of carcass sites. Similarly, *Agropyron smithii*, a cool-season perennial grass, became the overwhelming dominant at sites where it was initially present. However, warm-season grasses did not recolonize the center of carcass sites, possibly because of inhibition by elevated soil N (Tilman 1987). Low soil pH may also have been unfavorable for their establishment. The release of hydrogen ions during nitrification increases soil acidity (Wolcott et al. 1965). Low pH affects the availability of nutrients and, thus, can alter colonization patterns and plant community dynamics. Despite the high buffering capacity of the limestone soils, the reduced pH at carcass sites did not increase over time and may be an enduring impact of carcasses.

Successional dynamics around carcass sites are influenced by the severity of the disturbance. Colonization of large gaps in grasslands is strongly dominated by seedling establishment, whereas colonization of small gaps is predominantly from clonal growth of surrounding plants (Bullock et al. 1995). Although the exposed soil at carcass sites was revegetated rapidly with opportunistic plants, gap closure does not equate to recovery. The gradual decline of warm-season grasses in the inner 50 cm at juvenile carcass sites suggests that the surviving ramets were not competing successfully with the forbs. Five years after death, canopy cover of *Andropogon gerardii* was significantly lower in the center of all carcass sites than in the peripheral zone, indicating that reversion occurs very slowly. Platt (1975) surmised that it took more than 20 years for tallgrass prairie to recover from badger disturbances. The nutrient infusion from carcasses may prolong the time required before aboveground vegetation reverts to predisturbance conditions. The area underneath carcasses may also require extended time for recovery. Bornemissza (1957) observed that 1 year after death, the soil arthropod population under guinea pig (*Cavia porcellus*) carrion had not redeveloped. Thus, both aboveground and belowground processes are likely to be affected by ungulate carcasses for many years.

Species richness and diversity at the center of carcass sites were low initially but increased significantly the following 2 years after death as pioneer species colonized the area. However, both richness and diversity in the inner 50 cm were substantially lower than comparable measurements from undisturbed tallgrass prairie (Platt 1975; Gibson 1989). Elevated soil fertility reduces species richness and diversity by favoring opportunistic species that have a rapid growth rate (Huston 1979). Because many of these pioneer species do not normally occur in undisturbed prairie, carcass sites can increase community heterogeneity.

Vegetation adjacent to carcass sites likely contains high nutrient levels from growing in the enriched soil. Herbivores are attracted to patches of high-quality forage (Day and Detling 1990; Wallis de Vries and Daleboudt 1994), and many carcass sites in both bison and cattle pastures were grazed. The likelihood of repeated grazing near carcass sites provides a positive feedback of continual nutrient supplementation from dung and urine depositions (Hobbs 1996), which can expand the impact beyond the carcass boundary.

The significance of large herbivore carcasses as contributors to grassland dynamics and nutrient cycling becomes substantial when considered in a historical perspective. Episodic disasters such as severe droughts, harsh winters, or endemic diseases can produce high ungulate mortality (Seton 1906; Soper 1941). Roe (1970) reported numerous accounts of the overwhelming stench from rotting carrion that died in natural disasters. Additionally, the mass slaughter of bison in the 1800s littered the plains with millions of carcasses (Dary 1973). After cattle replaced bison as the predominant herbivores, mass catastrophes continued to punctuate normal mortality events. In Kansas alone, more than 272,000 cattle perished from successive winter blizzards in 1885 and 1886, and their carcasses were left on the prairie (Dary 1987; Wheeler 1992). Other severe winters, droughts, and periodic grasshopper swarms have similarly left thousands of cattle to starve and die in situ (Dary 1987). Currently, mass mortality of large ungulates is less common, but individuals continue to die of natural causes. Carcasses, both solitary and en masse, have enriched grasslands for eons and provided a continual cycle of disturbance and recovery.

In summary, this study indicates that herbivore carcasses represent a unique type of disturbance that may play an important role in adding spatial complexity in grassland ecosystems. Although they are relatively infrequent, the impact of ungulate carcasses on prairie vegetation is extremely intense. Unlike other natural disturbances, carcasses deposit a substantial amount of nutrients into the surrounding soil. Depending upon carcass size, this flux may either be concentrated in a small patch or dispersed over a wide area. Nitrogen input from carcasses may have important implications for the N balance of tallgrass prairie. By providing a nutrient-enriched site for fugitive or competitively suppressed species, carcasses also increase community heterogeneity. Although this study did not resolve questions of longevity and recovery, the disturbed areas created by ungulate carcasses are islands of fertility that likely will leave an indelible impression on the surrounding soil and vegetation for many years.

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